Parental care in the Common Tern (*Sterna hirundo*): sexual roles in a monogamous seabird

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ABSTRACT

The parental behaviour of male and female Common Terns (Sterna hirundo) was documented throughout two breeding seasons at a colony near Port Colborne, Ontario. Thirteen and fourteen pairs of terns were chosen for intensive study in 1982 and 1983, respectively. The delivery of fish by males to their mates ("courtship feeding") occurred prior-to, during, and following the egg-laying period. Following the laying of the second egg, courtship feeding rates declined significantly. There was a significant, positive correlation between courtship feeding rates and subsequent chick feeding rates by males.

The incubation rates of females were significantly higher than those of males, especially during the first ten days of incubation. Territorial attendance rates during the incubation stage were similar for males and females. During the chick stage, territorial attendance rates of females were significantly higher than those of males. The size of fish fed to chicks by males increased as the chicks grew older and chick feeding rates of males were approximately three times higher than female rates.

Based on these quantitative differences in parental care activities, the cumulative parental time investment by the two sexes was very similar. However, the energetic investment by males was likely greater than that by females, since male parental contributions (e.g. courtship feeding and chick feeding) often entailed extensive foraging behaviour.

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INTRODUCTION

Although over 90% of bird species breed monogamously (Lack 1968), the study of avian mating systems has largely centered on polygynous systems. Among seabirds, monogamy is the predominant mating system (Lack 1968, Wittenberger 1979), with polygyny occurring only rarely among gulls and skuas (Hunt 1980). The widespread occurrence of monogamy among seabirds likely occurs because active participation by both parents is normally required throughout each breeding attempt (Hunt 1980; but see Nisbet et al. 1978).

Current mating system theory focuses on the different reproductive interests of males and females (Emlen and Oring 1977, Wittenberger 1979, Hunt 1980). Because male gametes are considerably smaller and require much less energetic investment than female gametes (Walsberg 1983a), males are generally not restricted in gamete production and should be expected to mate with as many females as possible (Bateman 1948, Williams 1966, Fitch and Shugart 1984). Trivers (1972) proposed that this initial asymmetry in gametic investment predisposes females for providing the bulk of parental care, especially in monogamous species. According to Trivers, there are times when each sex has invested more than the other and at these times, the sex with the lowest cumulative investment is tempted to desert. Boucher (1977) and Dawkins and Carlisle (1976) criticized this reasoning, pointing out that the "decision" to desert cannot be made on the sole basis of past investment, but must also rest on future reproductive opportunities and the consequences of desertion on

the success of the deserted female.

In many species of seabirds, females are not able to raise young without some male assistance (Hunt 1980, Wittenberger 1981). In this case, males may realize higher reproductive success by providing paternal care, and, when possible, attemping "extrapair" copulations (Fitch and Shugart 1984). However, the reproductive opportunities of males may be restricted by the availability of potential mates. If female sexual receptivity occurs synchronously, as it often does among colonial seabirds, males may be temporally restricted in the number of copulations that they are able to obtain (Emlen and Oring 1977, Knowlton 1979, Gochfeld 1980). In addition, an extended courtship period is typical of many seabird species, thus further restricting the reproductive opportunities of males (Hunt 1980).

PARENTAL INVESTMENT

The concept of parental investment (PI) has been valuable in the formation of current mating system theory (Emlen and Oring 1977, Wittenberger 1979). Trivers defined PI as "any investment in an individual offspring that increases that offspring's chances of survival (and hence reproductive success) at the cost of the parent's ability to invest in other offspring". Such investment may be in the form of energy or time expenditure, or risk of predation and/or injury. Trivers included such variables as incubation of eggs and the brooding and feeding of chicks as forms of PI. He did not include efforts expended prior to fertilization, such as mate attraction and intrasexual

competition for access to members of the opposite sex, since these mating efforts do not normally affect offspring survival. Similarly, Low (1978) and Alexander and Borgia (1979) classified all such efforts expended prior to fertilization as mating effort, since they function to secure matings. However, among seabirds, efforts expended prior to fertilization often have an effect on offspring survival. For example, in many seabird species, intense male-male competiton for nest sites occurs prior to the arrival of females in the nesting area (Swales 1965, Bedard 1969, Nelson 1978a, Montevecchi and Porter 1980). The establishment of a preferred nest site increases the male's chances of obtaining a mate and may also attract higher quality (age, experience) females (Hunt 1980). Preferred nest sites also improve the chances of offspring survival (Parsons 1976, Pierotti 1982) and thus, male-male competition prior to fertilization may indeed have an effect on offspring survival. Accordingly, the classification of pre-zygotic behaviour into mating effort and parental investment is often difficult.

An additional difficulty with PI theory is that it is empirically difficult to quantify and virtually impossible to measure according to the relative magnitudes of its various forms (e.g. does defense of the territory constitute "more" parental investment than brooding behaviour?). In addition, different behaviour involves different currencies of PI, such as energy and risk, thus further complicating quantification. In his discussion of the energetics of avian reproduction, Walsberg (1983a) pointed out several difficulties in applying PI theory to

energetic estimates of parental care. The most important of these difficulties is in assessing whether parents are capable of allocating energy to future reproductions. Walsberg (loc. cit.) has shown that if a typical female passerine reduces her energy expenditure by 25% during a particular reproductive event for use in a subsequent reproduction, she would have to store a fat equivalent of 72% of her normal body mass. However, Walsberg did not consider the possibility of investing such energy in other immediate reproductive options (e.g. deserting the current mate and re-mating with a different male or female). Due to the difficulties outlined above, I prefer to use the term "parental care" rather than PI *per se*. Pierotti (1981) and Mundahl (1982) used a similar procedure. In describing the components of parental care, I use parental time investment and thus avoid confusing the currencies involved in parental care. Because courtship feedings and chick feedings could not be measured as a time component, I used the term "parental contribution" for these components of parental care.

COURTSHIP FEEDING

In many species of birds (references in Lack 1940, Royama 1966), males provide females with food (courtship feeding) prior to and during the egg laying stage. Traditionally, such provisioning was thought to serve only a symbolic function in strengthening the pair bond (Lack 1940). Indeed, early studies on passerines (Kluijver 1950, Andrews 1961) regarded such feeding as symbolic and without nutritional importance, since it occurred infrequently. However, these studies were based on observations

at the nest, whereas Royama (1966) found that the majority of courtship feedings by male Great Tits (Parus major) and Blue Tits (P. caeruleus) took place away from the nest site while females were foraging. Thus, Kluijver and Andrews may have been observing only a small proportion of the total feedings that were actually occurring.

Lack (1940) recognized that courtship feeding, when it occurred commonly during the laying and incubation periods, may serve more than just a symbolic function. Studies on the Pied Flycatcher (Muscicapa hypoleuca; Von Haartman 1958, Curio 1959, cited in Royama 1966) indicated that females receive substantial amounts of food from their mates during the egg formation period. More recently, Krebs (1970) found that female Blue Tits, during the egg formation period, received more food items per unit time when being fed by males than when foraging alone. This has important consequences since females that are able to take in more food are also able to breed earlier (Kallander 1974, Dijkstra et al. 1982) and thus, may realize higher reproductive success (Perrins 1965). It appears then, that courtship feeding may be an important form of male parental investment in some species of birds.

Courtship feeding has been observed in many species of marine birds including gulls (Lack 1940, Tinbergen 1953, Brown 1967, Hunt 1980, Tasker and Mills 1981), terns (Cullen and Ashmole 1963, Nisbet 1973, Moller 1981) and skuas (Stonehouse 1956 cited in Hunt 1980, Andersson 1971). Tasker and Mills (1981) made a detailed study of courtship feeding in the Red-billed Gull

(Larus novaehollandiae) and found that it served at least two functions. First, it provided essential nutrition to the female prior to and during egg laying and second, it served as an inducement to copulation.

Nisbet (1973, 1977) studied courtship feeding in Common Terns (Sterna hirundo) in Massachusetts and was particularly interested in the effects of courtship feeding on egg size, clutch size, and hatching and fledging success. He found that pairs with high rates of courtship feedings realized large egg and clutch sizes, as well as high hatching and fledging success. Thus, food furnished to females by males apparently contributed significantly to the nutritional reserves of females, with consequent reproductive benefits for both sexes. However, a significant correlation was not found between courtship feeding rates and chick feeding rates for these males. Thus, Nisbet's results did not exclude the possibility that the correlation between male courtship feeding rates and the weight of their mates clutches and broods was a result of "high quality" males pairing with "high quality" females.

Given the importance of courtship feeding to female nutrition during egg-laying, selection for mate choice by females, based on initial male courtship feeding performances, may be operating. Among monogamous larids, where parental contributions of the male and female are generally similar (Burger 1981, Pierotti 1981), courtship feeding performance provides a potential basis for female mate choice based on male "quality", given the following assumptions: 1) sufficient numbers

of males from which females may choose; 2) sufficient variation in male "quality"; 3) a positive correlation between the quality of male courtship feeding and subsequent paternal contributions to chick production; and 4) ability of females to discriminate and actively choose among males of varying quality (Halliday 1983).

Few studies have investigated the relationship between courtship feeding and paternal care. Niebuhr (1981) studied courtship feeding and subsequent paternal care in Herring Gulls (Larus argentatus) and found that courtship feeding rates were positively correlated with time spent incubating, time spent on the territory during the chick stage, and chick feeding frequency. As mentioned above, Nisbet did not find a significant correlation between courtship feeding rates and chick feeding rates by male Common Terns. The establishment of a link between courtship feeding quality and paternal care quality would provide a basis for potential mate choice by females, based on male parental quality.

The objective of my study was to quantify the parental care patterns of Common Tern parents during a breeding bout, and to relate these activities to predictions of parental care patterns in a monogamous species. In addition, I discuss the parental roles of each sex and the implications of these roles in functional terms.

METHODS

1. The Study Area

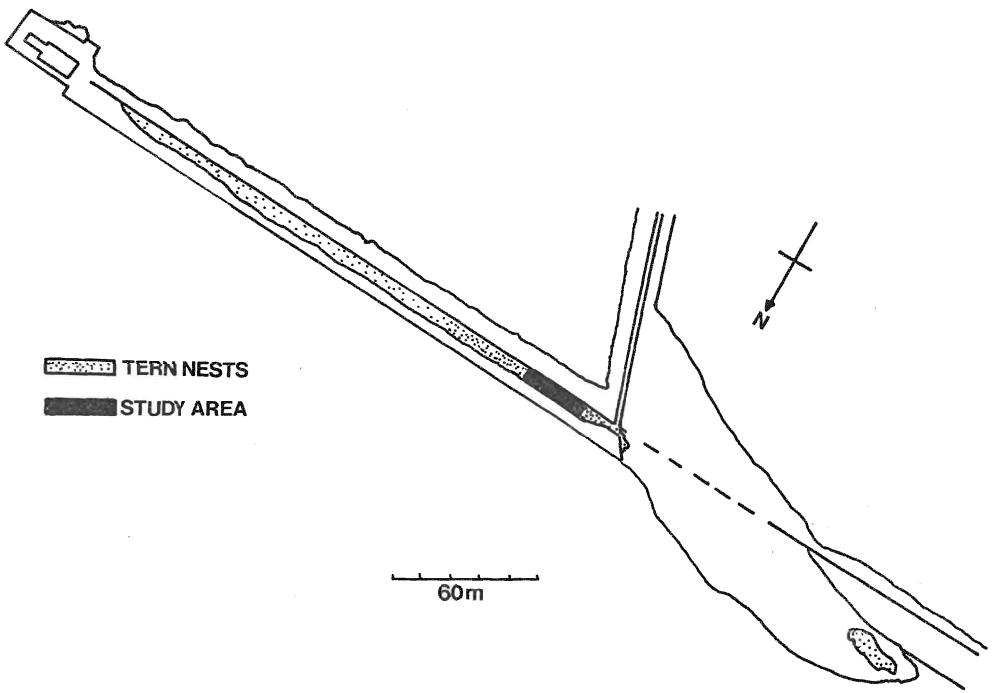
The study was conducted at a Common Tern colony near Port Colborne, Ontario (42 53' N, 79 16' W) on the north shore of Lake Erie. Common Terns nested on the eastern leg of a concrete breakwater complex approximately 1 km from shore (Fig. 1). In 1982 and 1983, terns occupied nest sites from the western end sequentially, to the eastern end of the shelf. In both years, the western end of the shelf was covered with small rocks and a small area of Mossy Stonecrop (Sedum acre). The eastern half of the shelf was sparsely covered with small, loose, concrete chips.

The same study area was used in both years (Fig. 1). This area was located near the western end of the shelf, adjacent to an elevated concrete wall and was approximately 15 m long and 3 m wide. The substrate within the study area was comprised of an earthen base covered with concrete chips, small logs, and scattered outcrops of S. acre. Except where noted, materials and methods were identical in the two years of study.

2. Data Collection

In late April, an elevated blind (4m X 4m X 4m) was erected in front of the study site, prior to the arrival of Common Terns in the Port Colborne area. Small numbers of adult Common Terns have been banded at the Port Colborne colony since 1976 and all study pairs (N=13, 1982; N=14, 1983) were chosen from pairs in which at least one bird had been banded previously. Trapping of adults was carried out in early May 1982, during the first week

Figure 1. Location of the study area and the distribution of Common Tern nests on the breakwall in 1982 and 1983.


TERN NESTS
STUDY AREA
60m
N

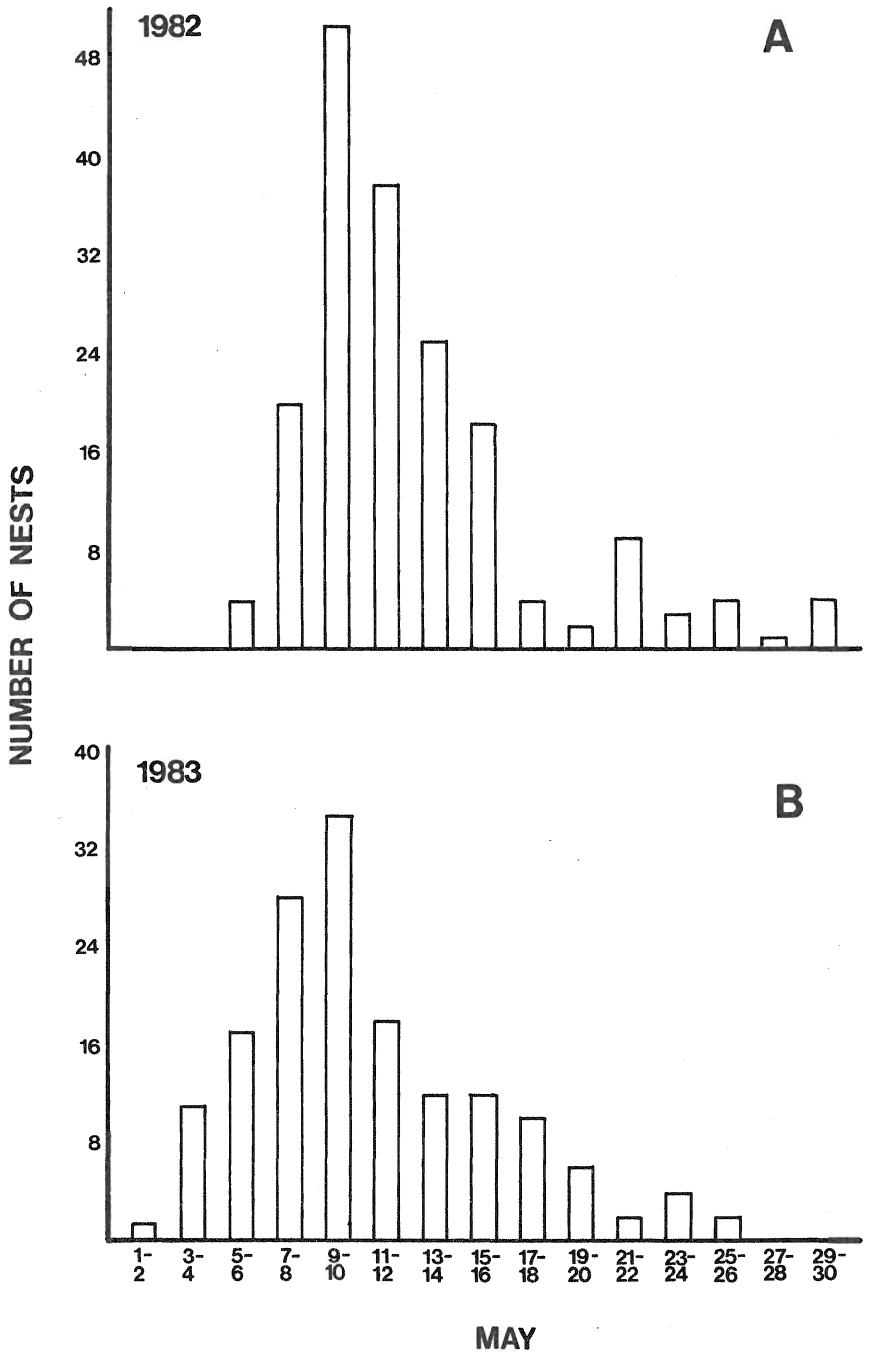
of incubation. Walk-in, chicken wire traps were placed over the 13 study nests and both members of each pair were captured while they incubated eggs. All birds were then color banded for individual identification. In no case did trapping cause desertion of the nest. In 1983, at least one member of each of the study pairs had been banded previously, thus allowing individual identification of pair members. The sex of pair members was determined by behavioural observations during the courtship period.

Study pairs were selected from those nesting during the peak of clutch initiations. Terns nesting during the peak period are generally older, more experienced breeders (Nisbet 1977, Hays 1978, Nisbet and Welton 1984). To determine the peak period of clutch initiations at the colony, daily nest checks were made along the entire length of the breakwall from late April through late May, 1982 and within the study area in 1983. The seasonal distribution of clutch initiations within the study area during the two years are presented in Figures 2a-b. At Port Colborne, the majority of nests initiated during the peak of egg laying were concentrated at the western end of the breakwall (including the study area; see Hunter 1976) where nest density was relatively high (4 nests/m^2).

Daily nest checks were made within the study area to ascertain the laying dates and clutch sizes of all pairs. Nest checks normally followed the observation periods in the blind and lasted approximately ten minutes. Other demographic data included egg fates, hatching success, chick fates and fledging success. To

Figure 2a. Frequency distribution of clutch initiations within the study area during May 1982. Days are pooled into two-day periods.

Figure 2b. Frequency distribution of clutch initiations within the study area during May 1983. Days are pooled into two-day periods.


1982
A
48
40
32
24
16
8
NUMBER OF NESTS
1983
B
40
32
24
16
8
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-16
17-18
19-20
21-22
23-24
25-26
27-28
29-30
MAY

prevent chicks from leaving the study area during these nest checks, a 35 cm high wire-mesh fence was erected around the site in late May. Nest checks were discontinued shortly thereafter to prevent disturbance.

Observations of parental care activities of study pair members began in late April and continued through the fledging of chicks from all study broods. Chicks reaching the age of 20 days were considered to have fledged as chicks are capable of flight and often move away from nest sites at this age (Hunter 1976). Observations were made daily from 1 May to 10 July 1982 and from 1 May to 24 July 1983. In 1982, observation periods were normally three hours in length, either during the early morning (05:30-09:00) or late afternoon (18:00-21:00). In 1983, observation periods were approximately eight hours/day during the first two weeks of May, and four hours/day for the remainder of the season (see Appendix 4b for summary of observation hours during each stage of the nesting cycle). In 1983, observations were made within the following periods: early morning (05:30-09:30); mid-day (10:00-15:00); and evening (17:00-21:00). For analytical purposes, the classification of observation periods into temporal components was determined as follows: AM= 05:30-09:30, MID=10:30-15:00, PM=17:00-21:00.

Data on parental activities at each of the study nests were collected over the entire nesting period of each pair. These activities included: 1) the rate of delivery and size (length; recorded in 1983 only) of fish fed to females by their mates (courtship feedings); 2) the occurrence of mounting (male

standing on a female's back) and copulations (cloacal contact following mounting); 3) time spent incubating by each pair member; 4) size (length) and rate of delivery of fish fed to chicks by each pair member; and 5) territorial attendance (excluding incubation) during the incubation and chick stages. The size of fish delivered to females and chicks was estimated to 0.5 bill units using the adult's bill as a template. In addition, courtship feedings were recorded for unmarked pairs within the fenced study area during the egg-laying period.

3. Statistical Treatment

Prior to the application of statistical tests, all data sets were tested for normality (skewness and kurtosis tests, Kolmogorov-Smirnov Test; Sokal and Rohlf 1981) and homogeneity of variances (Bartlett's Test of homogeneity of variances and/or Fmax-test; Sokal and Rohlf, loc. cit.). When all data sets within a group (e.g. courtship feeding rates, mean rates of incubation) conformed to these parametric assumptions, parametric analyses were used. When parametric assumptions were not met, data were analyzed either with non-parametric tests, or were transformed to meet parametric assumptions. Because the time-budget data consisted of proportions (which are rarely normally distributed), time budget data were transformed using the arc-sine method (Sokal and Rohlf 1981). When Mann-Whitney U tests and Wilcoxon Signed Ranks tests were used, probabilities were determined from the Z statistic (Siegel 1956).

RESULTS

Variation in clutch sizes may reflect age and/or breeding experience differences among parents (Ryder 1980). Accordingly, in the first two sections of results (courtship feeding and incubation), males whose mates laid two-egg clutches (2-egg males) were treated separately from males whose mates laid three-egg clutches (3-egg males). The classification of observation periods into temporal components was determined as follows: AM=05:30-09:30, MID=10:00-15:00, PM=17:00-21:00.

1. COURTSHIP FEEDING

At Port Colborne, the delivery of fish by males to their mates was rarely observed at the nest site earlier than three days prior to clutch initiation. Consequently, for courtship feeding analyses, the pre-laying period consisted of the three days (Days -3 through -1) prior to clutch initiation (Day 0); the 1-2 egg period was Day 0 through the laying of the second egg; the 2-3 egg period was the remainder of the laying period (ie. through clutch completion). In 1982, the length of daily observations from the blind during the courtship feeding period was short (3 hours/day) relative to 1983 (8 hours/day). In addition, observations of courtship feedings during the pre-laying period were not made for all study pairs in 1982. Consequently, courtship feeding rates in the following analyses are based on data collected in 1983.

A. Temporal Patterns of Courtship Feeding

Courtship feeding rates (CFR) were analyzed for temporal

differences, corresponding to the 3 diurnal observation periods (Appendix 1a). AM rates were significantly higher than both MID and PM rates. MID and PM rates were not significantly different. As a consequence of the difference in the timing of clutch initiations among the study pairs (Appendix 1b), the individual totals of MID period observation hours were extremely variable between males (range: 0-22.8 hours/male). Consequently, MID period CFR were not used in subsequent analyses. AM and PM period CFR showed a significant positive correlation (Spearman Rank Correlation: $r=0.77$, $p < 0.01$, $N=13$) and, hence, were pooled for subsequent courtship feeding analyses.

Males delivered fish of varying lengths to their mates (Figure 3). For the period from Day -3 to clutch completion, fish length and rate of courtship feedings were not significantly correlated (Spearman Rank Correlation: $r=-0.22$, $p > 0.05$, $N=14$). Thus, males that delivered relatively small fish to their mates did not compensate by delivering fish at a higher rate.

The rate of courtship feedings by males of the 14 study pairs, relative to the stage of clutch completion, is shown in Figure 4. For unmarked 3-egg males within the study area, CFR were available only during the laying period as identification of pair members prior to the laying period was not possible. For 2-egg males, CFR peaked prior to clutch initiation, remained relatively high through clutch completion, then declined. For 3-egg males, CFR peaked during the 1-2 egg period, declined rapidly, then remained near zero following clutch completion. Similarly, CFR of unmarked 3-egg males declined from the 1-2 egg

Figure 3. The mean (± 1 S.E.) rate (feeds/hr.) of courtship feeding relative to the length of fish delivered to the female during the period from Day -3 to clutch completion. Sample sizes for fish lengths are above or below standard error bars. Data are from 1983 only.

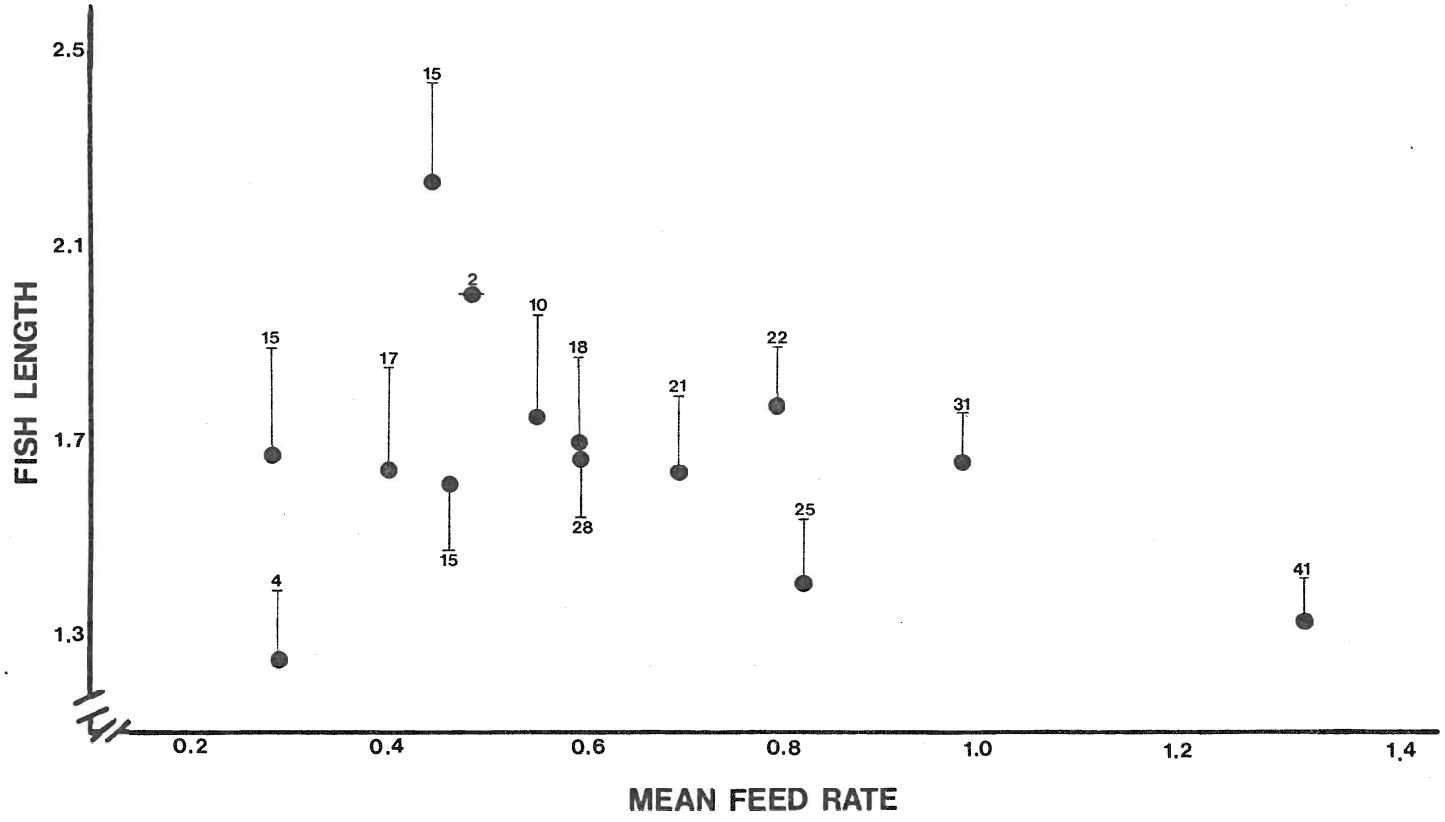
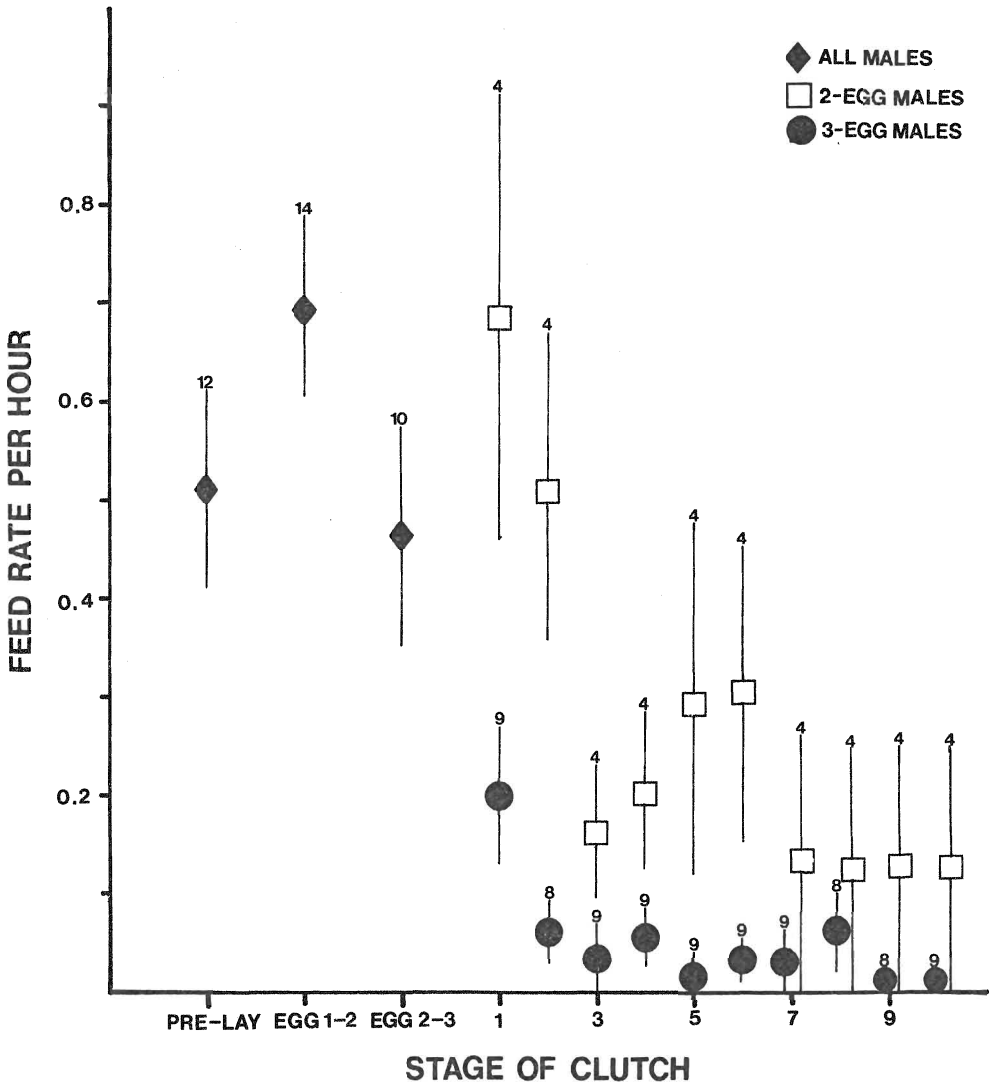

FISH LENGTH
2.5
2.1
1.7
1.3
0.2
0.4
0.6
0.8
1.0
1.2
1.4
MEAN FEED RATE
15
2
10
15
17
18
22
21
31
28
25
4
41

Figure 4. Mean (± 1 S.E.) courtship feeding rates (feeds/hr.) relative to the stage of clutch completion in 1983. The pre-laying period represents the three days prior to clutch initiation and the Eggs 1-2 and 2-3 periods represent the intervals between the laying of those eggs. Numbers following the Egg 2-3 period represent the days after clutch completion. Sample sizes appear above the standard error bars.


ALL MALES
2-EGG MALES
3-EGG MALES
FEED RATE PER HOUR
0.8
0.6
0.4
0.2
PRE-LAY
EGG 1-2
EGG 2-3
1
3
5
7
9
STAGE OF CLUTCH

period through clutch completion.

Among 2-egg males, CFR during the pre-laying period were not significantly different from those between the laying of the first and second eggs (Table 1). Among marked 3-egg males, CFR were significantly higher during the 1-2 egg period than during the pre-laying and 2-3 egg periods. CFR during the pre-laying and 2-3 egg periods were not significantly different (Wilcoxon Two-Sample test: $U=50.5$, $p > 0.05$, $N1=9, N2=10$). Among unmarked 3-egg males, CFR during the 1-2 egg period were significantly higher than those during the 2-3 egg period.

When compared over the pre-laying and 1-2 egg periods, CFR of 2-egg males were not significantly different from those of 3-egg males (Mann-Whitney U-test: $Z=0.57$, $p > 0.05$, $N1=4, N2=10$). For the ten day period following clutch completion, CFR of 2-egg males were significantly higher than those of marked 3-egg males (Mann-Whitney U-test: $Z=2.47$, $p < 0.05$, $N1=4, N2=9$).

B. Courtship Feeding and Copulations

Between-year comparisons of mounting and copulation rates for 3-egg males revealed no significant differences either during the pre-laying or the laying periods (laying period=Days 1-3 following clutch initiation; Appendix 1c). Consequently, mounting and copulation data for the two years were pooled. Mountings and copulations were extremely rare following the laying period and, thus, data for this time period were not included in the analysis.

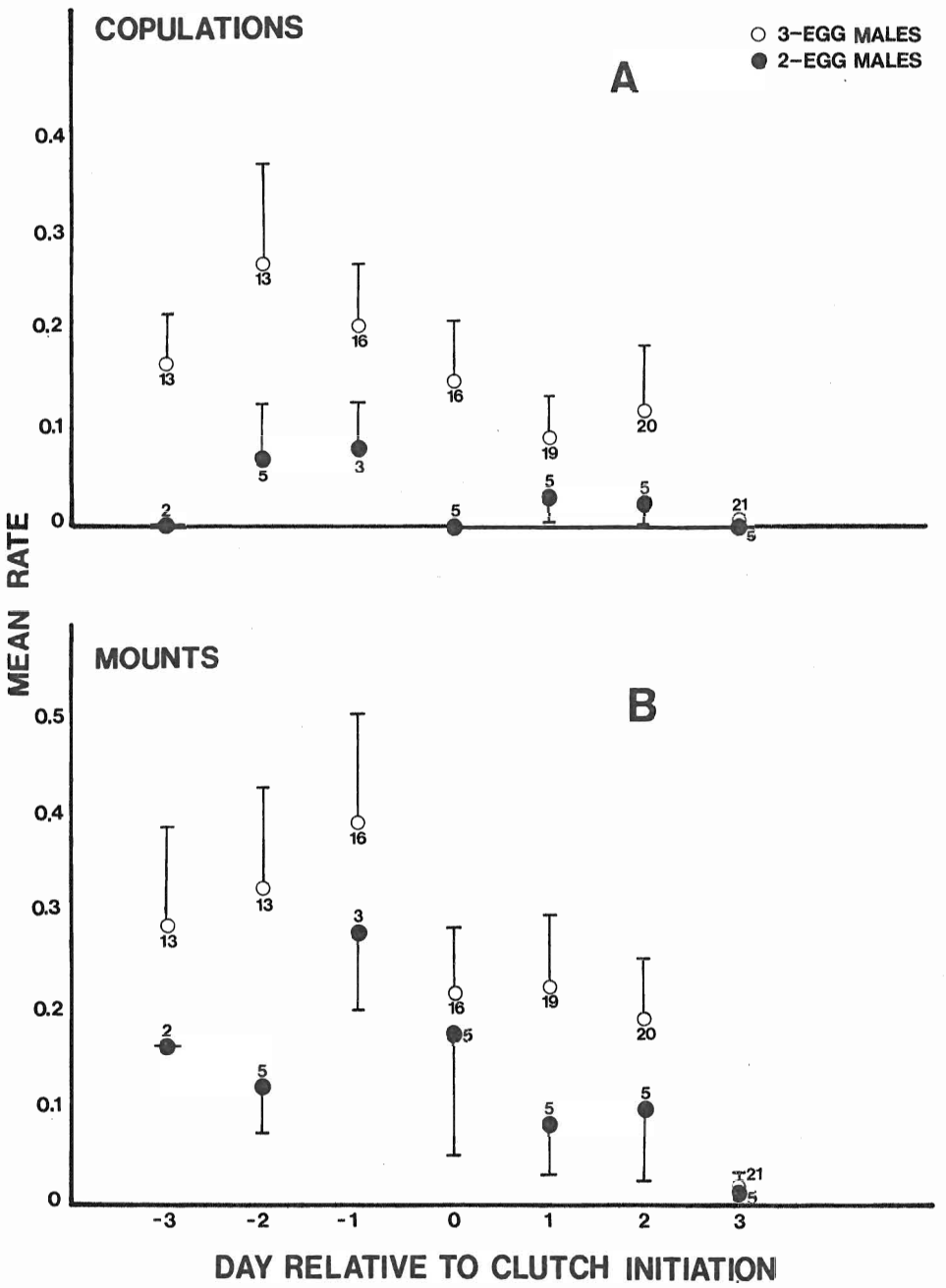
The mean copulation and mounting rates for 2-egg and 3-egg males are shown in Figures 5a-b. Among 2-egg and 3-egg males,

Table 1. Courtship feeding rates among 2-egg, marked 3-egg, and unmarked 3-egg males. Comparisons are between the pre-laying, 1-2 egg, and 2-3 egg periods. All data are from 1983. Differences were tested with the Wilcoxon two-sample test (U) and the Wilcoxon signed ranks test (Z).

	PRE-LAY			EGGS 1-2					EGGS 2-3				
	N	X	S.D.	N	X	S.D.	U	P	N	X	S.D.	Z	P
2-egg Males	3	0.83	0.09	4	0.69	0.52	9	>0.05			-		
Marked, 3-egg Males	9	0.41	0.32	10	0.71	0.30	68	<0.05	10	0.46	0.34	2.31	<0.05
Unmarked, 3-egg Males		-		42	0.44	0.26			42	0.26	0.20	3.43	<0.001

Figure 5a. Mean (± 1 S.E.) copulation rates (# copul./hr.) as a function of day relative to clutch initiation for 2-egg males and 3-egg males. Day 0 represents the day of clutch initiation. Data are pooled for 1982 and 1983. Sample sizes are adjacent to each mean.

Figure 5b. Mean (± 1 S.E.) mounting rates (# mounts/hr.) as a function of day relative to clutch initiation for 2-egg and 3-egg males. Day 0 represents the day of clutch initiation. Data are pooled for 1982 and 1983. Sample sizes are adjacent to each mean.


COPULATIONS
3-EGG MALES
2-EGG MALES
A
MOUNTS
B
MEAN RATE
0
0.1
0.2
0.3
0.4
0.5
-3
-2
-1
0
1
2
3
DAY RELATIVE TO CLUTCH INITIATION

mean rates of mounting and copulation were not significantly different between the pre-laying and laying periods (Appendix 1d). Although mounting and copulation rates were consistently higher for 3-egg males during both the pre-laying and laying periods, statistical comparisons of these rates between 2-egg and 3-egg males yielded no significant differences during either the pre-laying or laying periods (Appendix 1e).

Table 2 summarizes the effect of courtship feedings on the occurrence of copulations during the pre-laying and laying periods. For 3-egg males, the number of copulations that were preceded by courtship feedings was not significantly different when compared between the pre-laying and laying periods during 1982 or 1983. When data for the two years were pooled, the number of copulations that were preceded by courtship feedings was significantly higher during the laying period than during the pre-laying period (Table 2). The occurrence of courtship feedings did not have a significant influence on the success of mounts during either the pre-laying or laying period (Table 3). Similar data for 2-egg males were not analyzed as the number of courtship feedings prior to copulations by 2-egg males were limited (N=2).

C. Courtship Feeding and subsequent Paternal Care

Spearman Rank Correlations between CFR and subsequent male contributions to chick care are presented in Table 4. Because brood sizes remained constant through Day 12 of the chick stage, parental attendance rates during the chick stage and chick feeding rates were computed from Days 1 through 12 inclusive.

Table 2. Comparison of the number of copulations preceded by courtship feedings during the pre-laying and laying periods. Data are for 3-egg males only. Comparisons were made with 2 X 2 contingency Chi-square tests or with Fisher's Test.

	Number of copulations not preceded by courtship feeding	Number of copulations after courtship feedings	χ^2	p
1982				
Pre-laying	7	0	1 F	< 0.05
Laying	3	5		
1983				
Pre-laying	15	3	5.23	< 0.05
Laying	14	14		
Pooled				
Pre-laying	22	3	10.64	$= 0.001$
Laying	17	19		

1 Fisher's Exact probability test.

Table 3. The influence of courtship feeding on the success of mounts during the pre-laying and laying periods. Data are pooled from 1982 and 1983 for 3-egg males. Comparisons were made with 2X2 contingency Chi-square tests.

	Number of mounts	Followed by copulation	Not followed by copulation	χ^2	P
Pre-laying					
Courtship feeding	9	3	6	0.95	>0.05
No courtship feeding	43	22	21		
Laying					
Courtship feeding	29	19	10	1.85	>0.05
No courtship feeding	35	17	18		

Table 4. Spearman Rank Correlation Coefficients between courtship feeding rates (CFR) and subsequent paternal contributions for males in 1983. Sample sizes in parentheses.

	Incubation min./hr.	Territory attendance egg stage min./hr.	Territory attendance chick stage min./hr.	Chick feeds /hr.
CFR	-0.22[a] (13)	0.10[a] (13)	-0.15[a,c] (7)	0.92[b,c] (7)

a $P > 0.05$

b $P < 0.01$

c Only those males raising three chick broods were used in the analysis.

CFR were not significantly correlated with subsequent male incubation rates. Similarly, CFR were not significantly correlated with male territorial attendance (excluding incubation) rates during the egg and chick stages. However, the correlation between CFR and the delivery rates of fish to chicks by males was positive and significant.

2. THE INCUBATION STAGE

I defined the effective period of incubation behaviour as the day following clutch completion through the day prior to the hatching of the first chick. These limits were chosen because courtship feeding behaviour is common prior to clutch completion, and chick care behaviour begins once the first chick has hatched.

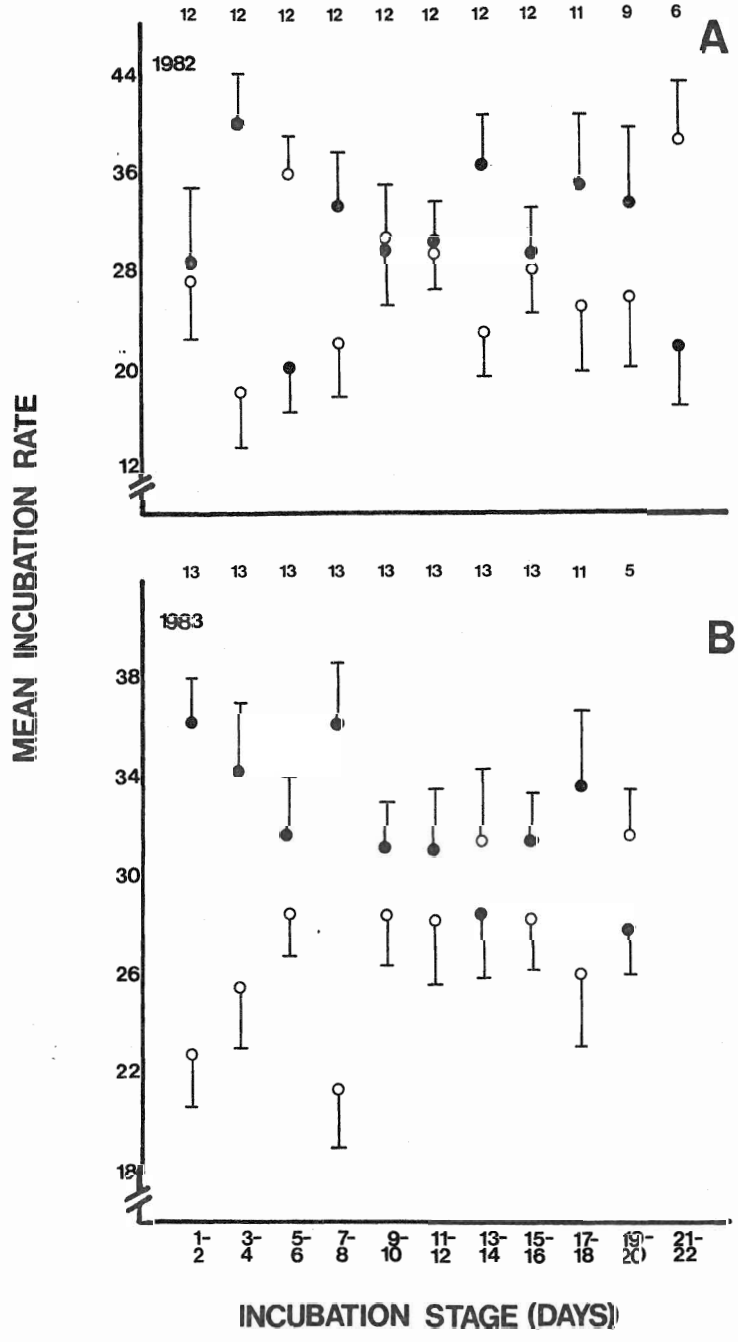
For the two study years, incubation lasted 16-23 days (mean = 20.15 $\pm$ 1.99; N=25). Using pooled data for the two years, there were no significant differences between the incubation rates of 2-egg and 3-egg females or mals (Appendix 2a). Similarly, there were no significant differences between the territorial attendance rates of 2-egg and 3-egg females or males (Appendix 2b). MID period watches during the incubation period were infrequent in both years (Appendix 2c) and, thus, were not included in the following analyses. Incubation rates were transformed by the arc-sine method for the analyses that follow.

A. Incubation Rates

The mean rates (minutes/hour) of incubation by males and females in 1982 are shown in Figure 6a. Males (mean=27.35 $\pm$ 5.07; N=12) and females (mean=30.94 $\pm$ 5.17; N=12) incubated with

Figure 6a. Mean (± 1 S.E.) incubation rates (mins./hr.) of males (O) and females (●) during two-day periods throughout the incubation stage. Days are numbered relative to the day of clutch completion (Day 0). Data are for 1982. Sample sizes are above the means for each period.

Figure 6b. Mean (± 1 S.E.) incubation rates (mins./hr.) of males (O) and females (●) during two-day periods throughout the incubation stage. Days are numbered relative to the day of clutch completion (Day 0). Data are for 1983. Sample sizes are above the means for each period.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11-12
13-14
15-16
17-18
19-20
21-22
MEAN INCUBATION RATE
INCUBATION STAGE (DAYS)

approximately equal frequency throughout the incubation period. Within-sex AM/PM differences in mean incubation rates are summarized in Table 5. In 1982, there were no differences in the mean incubation rates between AM and PM periods among females or among males. Furthermore, the difference between pooled AM and PM incubation rates was not significant when compared between the sexes (Wilcoxon Signed Ranks Test: $Z=1.33$, $p > 0.05$, $N=12$).

The mean rates of incubation by males and females in 1983 are in Figure 6b. Differences between the sexes in incubation rates were more pronounced than in 1982 with females (mean= 32.99 $\pm$ 2.71 mins.) incubating more often overall than males (mean= 26.55 $\pm$ 3.15 mins.). Prior to Days 9 and 10, female incubation rates were generally higher than those of males. Between Days 9 and 20, incubation rates by the two sexes were similar. In 1983, females incubated significantly more during PM periods than during AM periods while males incubated significantly more during AM periods than during PM periods (Table 5). However, when data for the two years were pooled, there were no significant differences between AM and PM incubation rates within the sexes (Table 5). Pooled AM/PM female incubation rates were significantly higher than pooled male rates (Wilcoxon Signed Ranks Test: $Z=3.11$, $p < 0.01$, $N=13$). This difference was largely due to intersexual differences in the pooled PM period rates when the two years were pooled ($Z=2.90$, $p < 0.01$, $N=13$) as the pooled AM period rates were not significantly different ($Z=0.87$, $p > 0.05$, $N=13$). The higher female incubation rates cannot be attributed to reduced incubation by 2-egg males relative to 3-egg

Table 5. Differences in AM and PM period incubation rates (minutes/hour) for males and females in 1982, 1983, and the two years pooled. Rates were computed over the entire incubation stage for each bird. T-tests were performed on arc-sin transformed data.

	Mean Rate (mins./hr.)	S.D.	t[1]	p	df
1982					
Females					
AM	32.00	7.29	0.46	>0.05	11
PM	29.98	9.38			
Males					
AM	27.42	6.93	0.03	>0.05	11
PM	27.36	8.70			
1983					
Females					
AM	31.10	3.83	2.81	<0.05	12
PM	35.32	4.30			
Males					
AM	27.89	4.75	2.16	<0.05	12
PM	24.53	4.43			
POOLED					
Females					
AM	31.53	5.65	0.66	>0.05	24
PM	32.76	7.55			
Males					
AM	27.66	5.77	0.88	>0.05	24
PM	25.89	6.82			

1 Paired t-test for related samples.

males as the mean incubation rates of the two groups were not significantly different ($t=0.64$, $p > 0.05$, $df=11$). Within-sex differences between the two years were not significant for either sex when AM/PM data were pooled (Table 6).

The mean rates of incubation by males and females, when data for the two years were pooled, are shown in Figure 7. When compared within two-day periods, incubation rates by the sexes were significantly different only during the Days 3-4 and 7-8 periods (Appendix 2d). However, when incubation rates for the entire incubation period were compared, female rates were significantly higher than those of males (Table 7).

In summary, male and female incubation rates were similar in 1982, both temporally and over the course of the incubation stage. However, in 1983, female incubated more during PM periods and over the course of the incubation stage. Overall, female incubation rates were significantly higher than those of males during the two years, especially during the early stages of incubation.

B. Territorial Attendance during Incubation

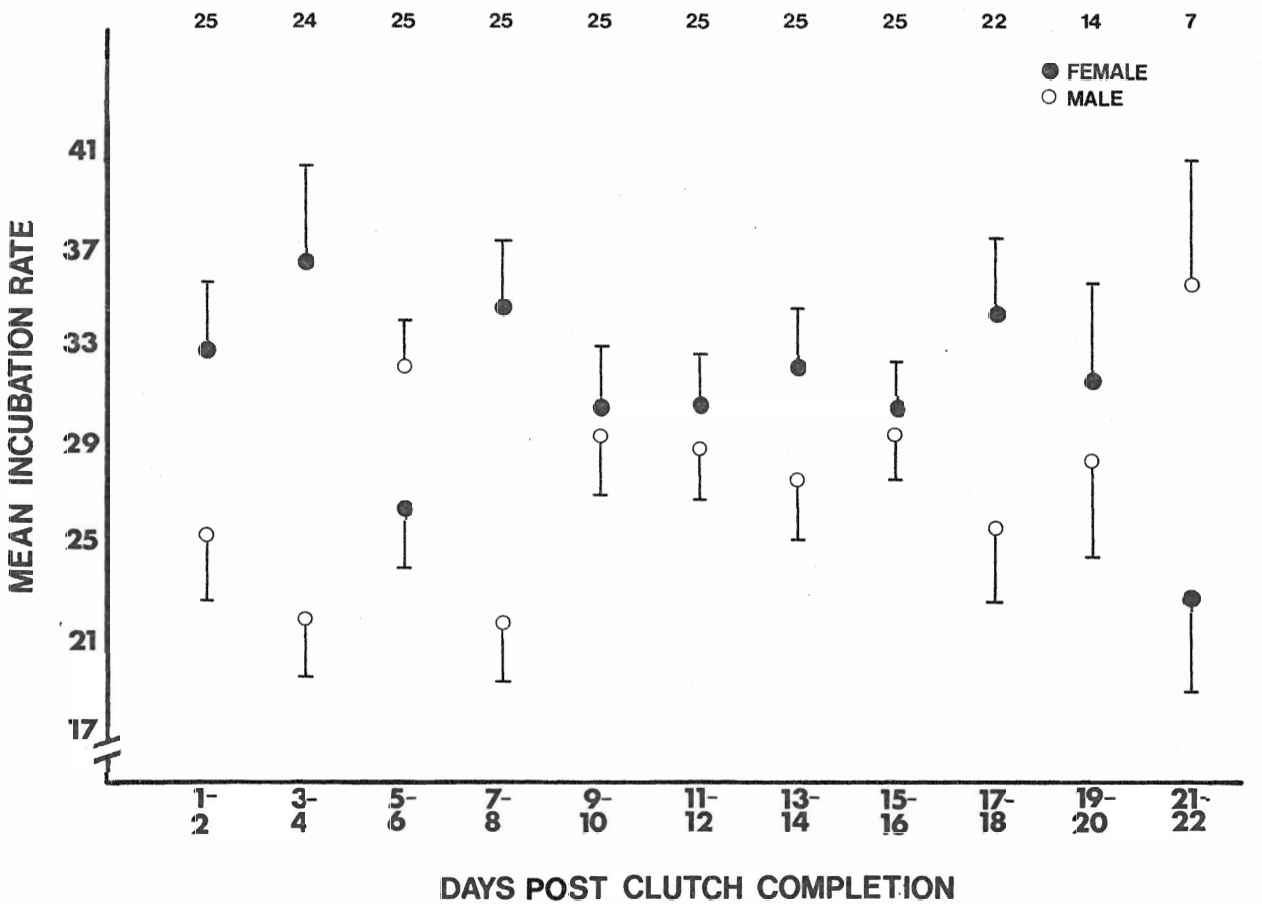
The amount of time that males and females spent at the nest site while not incubating (territorial attendance), was determined in both years. Using pooled attendance data for the two years, 2-egg and 3-egg pairs showed no significant differences in attendance rates within the sexes (Mann-Whitney U-test, males: $U=11$, $Z=1.08$, $p > 0.05$; females: $U=8$, $Z=1.54$, $p > 0.05$, $N=23$). Consequently, 2-egg and 3-egg pairs were pooled for subsequent analyses.

Table 6. Between-year differences in incubation rates within the sexes. Means were computed over the entire incubation stage of each individual. Data are pooled from AM and PM periods. Means are rates (mins./hour) following arc-sine transformations.

	Mean	S.D.	t[1]	p	df
Female					
1982	1.09	0.20	1.19	> 0.05	23
1983	1.17	0.11			
Male					
1982	0.95	0.19	0.52	> 0.05	23
1983	0.92	0.12			

1 Student's t-test

Figure 7. Mean (± 1 S.E.) incubation rates (mins./hr.) of males and females during two-day periods throughout the incubation stage. Days are numbered relative to the day of clutch completion (Day 0). Data are pooled from 1982 and 1983. Sample sizes are above the means for each period.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25
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14
7
FEMALE
MALE
41
37
33
29
25
21
17
MEAN INCUBATION RATE
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-16
17-18
19-20
21-22
DAYS POST CLUTCH COMPLETION

Table 7. Comparison of mean incubation rates of males and females over the entire incubation period. Data are pooled from 1982 and 1983. Comparison was made with the Wilcoxon Signed Ranks test.

	N	Mean Rate (mins./hr.)	S.D.	Z	p
Female	25	32.01	4.13		
				3.11	< 0.01
Male	25	26.93	4.11		

Since comparisons of pooled AM/PM attendance rates between years revealed significantly higher attendance rates during 1983 among both males and females (Table 8), territorial attendance data for the two years were not pooled for analysis. There were no significant differences in diurnal attendance rates within the sexes in 1982 (Wilcoxon Matched Pairs Signed Ranks Test: Females: $Z=1.96$, $p > 0.05$, $N=12$; Males: $Z=1.88$, $p > 0.05$, $N=12$) or in 1983 (Females: $Z=0.38$, $p > 0.05$, $N=13$; Males: $Z=0.38$, $P > 0.05$, $N=13$). Mean territorial attendance rates of males and females during the incubation periods of 1982 and 1983 are presented in Figures 8a and 8b, respectively. Within both years, there were no significant differences in male and female attendance rates during AM, PM, and POOLED AM/PM periods (Table 9).

3. CHICK CARE

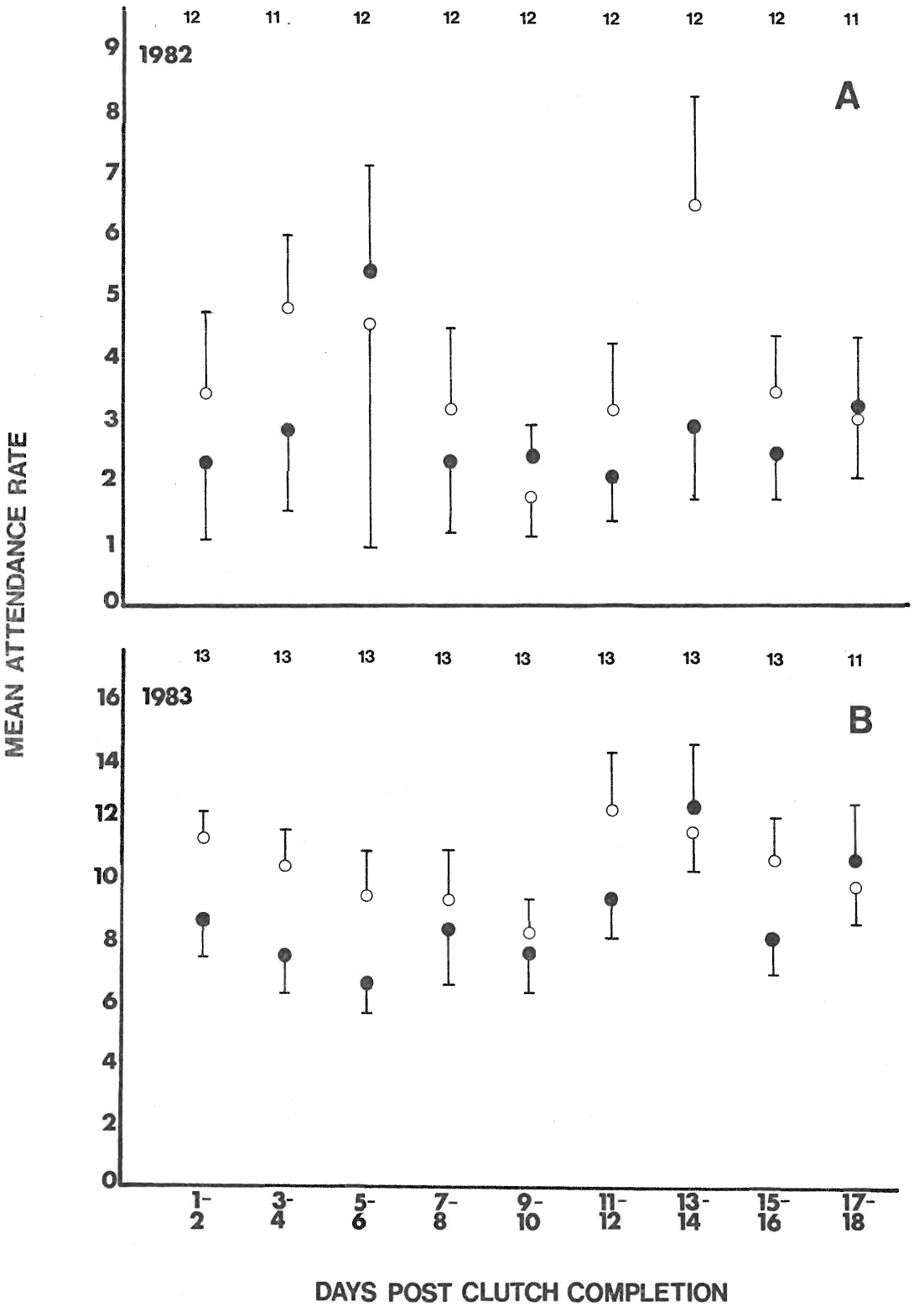
In 1982 and 1983, the mean interval between the hatching of the first and last chicks was 1.11 ± 0.60 days for two chick broods (N=9) and 2.29 ± 0.99 days for three chick broods (N=14). Because parental care during this period was directed at both eggs and chicks, analyses of chick feedings and chick attendance were begun on the day the last chick hatched (Day 1) and continued through Day 12 or Day 16. Feeding and attendance rate estimates throughout the entire period of chick care were complicated by decreasing brood sizes. A few chicks wandered from nest sites for several hours and occasionally for several days. These departures were normally caused by disturbances due to Herring Gulls and human activities near the colony site. Brood

Table 8. Between-year comparisons of pooled AM/PM territorial attendance rates within the sexes during the incubation stage. Comparisons were made with Mann-Whitney U-tests and only the smallest U values are given.

	N	U	Z	p
Female	12,13	7	3.86	< 0.001
Male	12,13	1	4.19	< 0.001

Figure 8a. Mean (± 1 S.E.) territorial attendance rates (mins./hr.), relative to the number of days following clutch completion (Day 0), of males (●) and females (○) during the incubation stage in 1982.

Figure 8b. Mean (± 1 S.E.) territorial attendance rates (mins./hr.), relative to the number of days following clutch completion (Day 0), of males (●) and females (○) during the incubation stage in 1983.


12 11 12 12 12 12 12 12 11
1982
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1983
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1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-16
17-18
MEAN ATTENDANCE RATE
DAYS POST CLUTCH COMPLETION

Table 9. Wilcoxon Signed Ranks Tests comparing sexual differences in mean territorial attendance rates during incubation. Comparisons are made within diurnal periods in 1982 and 1983 using the Wilcoxon Matched Pairs Signed Ranks test.

	N	Z	p
1982			
AM	12	0.55	>0.05
PM	12	1.41	>0.05
POOLED	12	1.41	>0.05
1983			
AM	13	1.15	>0.05
PM	13	1.92	>0.05
POOLED	13	1.92	>0.05

sizes in both years were relatively constant from the time the last chick hatched to Day 12 and, consequently, this period was emphasized in the chick care analyses. Following Day 16, chicks often left the nest site permanently and parental care, therefore, was difficult to quantify.

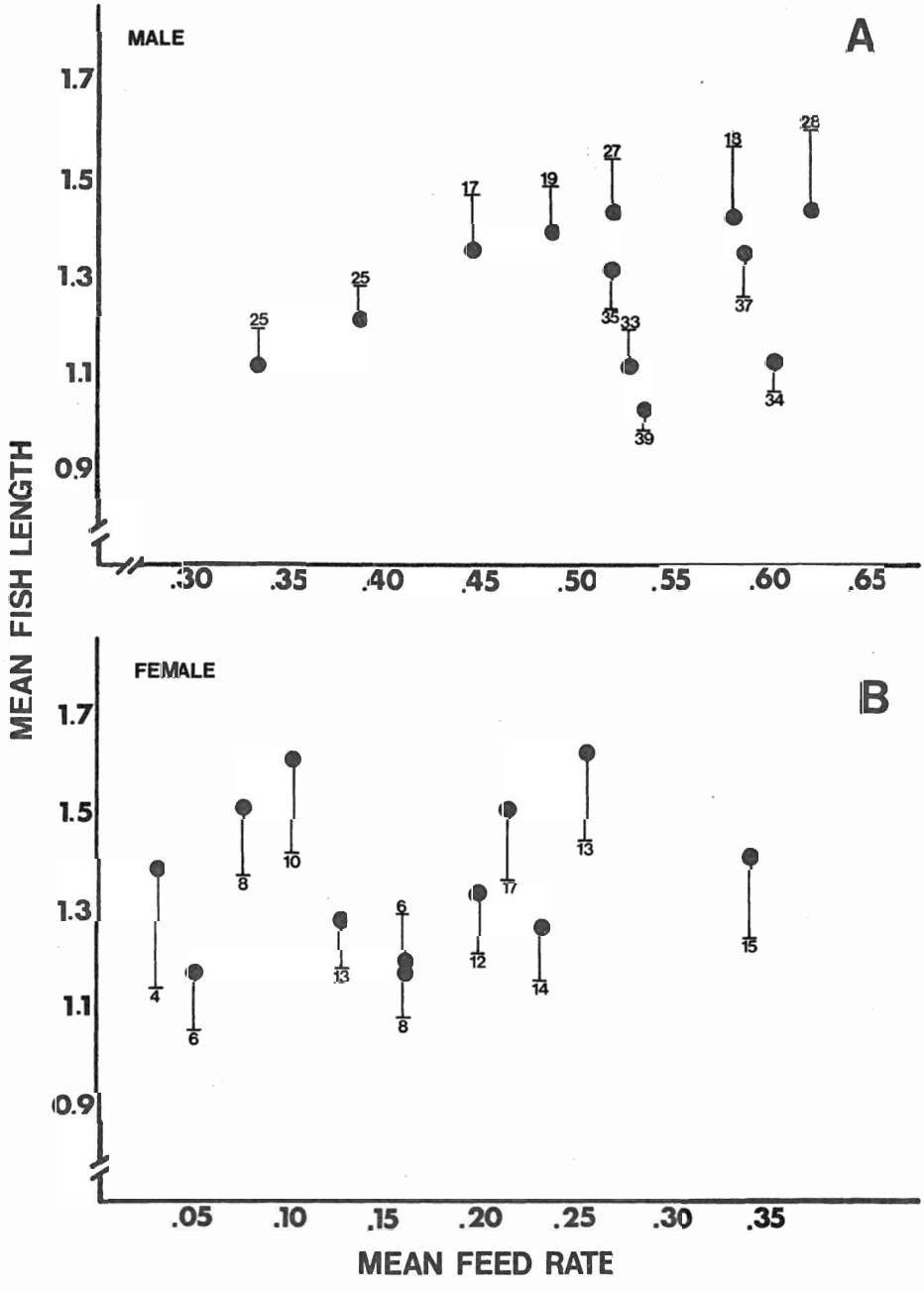
A. Chick Feeding Patterns

To control for variation in chick feeding rates due to different brood sizes, I measured feeding rates according to brood size (i.e. feeds/chick/hour rather than chick feeds/hour). Data on the length of fish delivered to chicks were collected only in 1983. Figures 9a-b show the relationship between the mean number of chick feedings/chick/hour by each parent and the mean size of fish delivered to chicks by those parents. The rate of chick feedings was not significantly correlated with the length of fish delivered by either sex (Appendices 3a-b; Spearman Rank Correlations; Females: $r=0.10$, $p > 0.05$, $N=11$; Males: $r=0.24$, $p > 0.05$ $N=13$). The lengths of fish delivered to chicks, relative to the day following last hatch, are shown in Figures 10a-b. The mean length of fish delivered to chicks by females varied considerably throughout the 12 day period. The length of fish delivered by males increased at Day 6 and remained relatively constant thereafter. There was no significant difference for females in the mean length of fish delivered to chicks between Days 1-6 and 7-12 ($t=0.42$, $p > 0.05$, $N1=47, N2=79$). The difference between the same two periods was significant for males ($t=3.65$, $p < 0.01$, $N1=183, N2=153$).

B. Male/Female differences in chick feeding

Figure 9a. The mean (± 1 SE) number of chick feedings/chick/hour by males relative to the length (# of bill lengths) of fish delivered to chicks. Data are from 1983 and from Days 1-12 following the hatching of the last chick. Rates of males feeding different sized broods were pooled. Sample sizes of fish length are above or below each standard error bar.

Figure 9b. The mean (± 1 SE) number of chick feedings/chick/hour by females relative to the length (# of bill lengths) of fish delivered to chicks. Data are from 1983 and from Days 1-12 following the hatching of the last chick. Rates of females feeding different sized broods were pooled. Sample sizes of fish length are above or below each standard error bar.


MALE
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.30
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FEMALE
B
.05
.10
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.20
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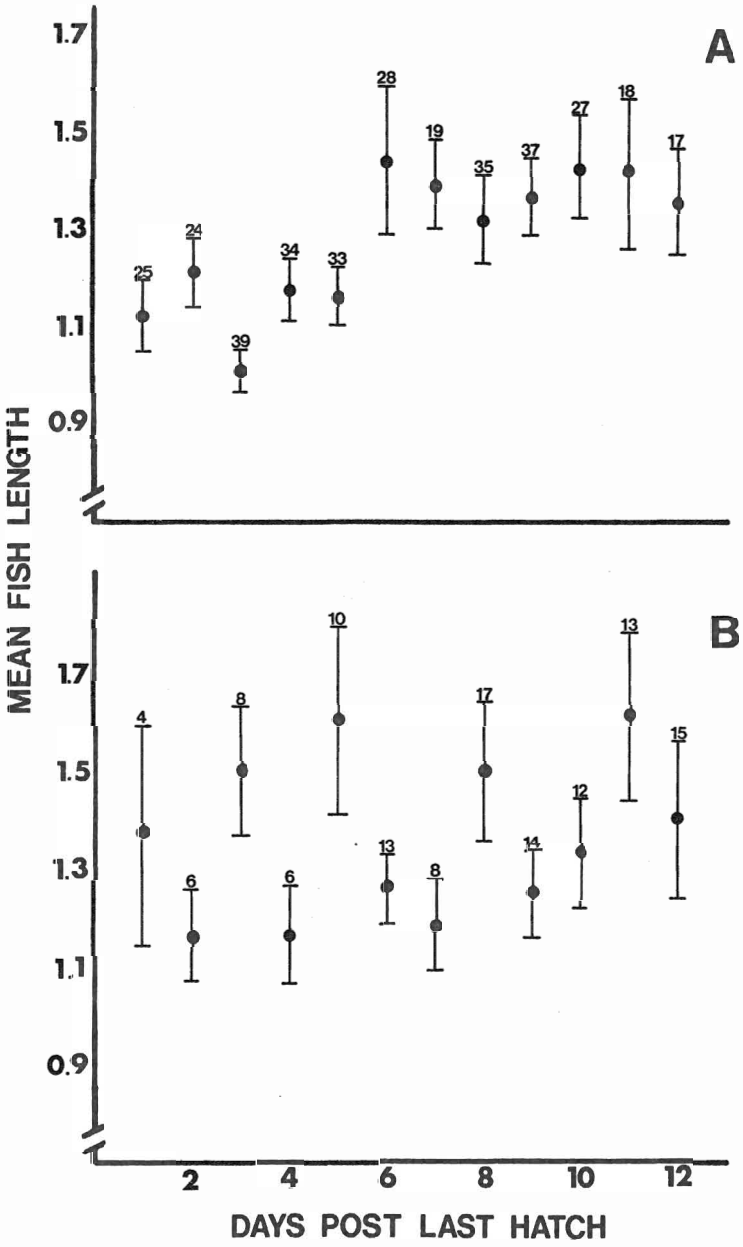
.35
MEAN FISH LENGTH
MEAN FEED RATE

Figure 10a. The mean (± 1 SE) length (# bill lengths) of fish delivered to chicks by males relative to the number of days following the hatching of the last chick. Data are from 1983 and from Days 1-12 following the hatching of the last chick.

Figure 10b. The mean (± 1 SE) length (# of bill lengths) of fish delivered to chicks by females relative to the number of days following the hatching of the last chick. Data are from 1983 and from Days 1-12 following the hatching of the last chick.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MEAN FISH LENGTH
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13
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2
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6
8
10
12
DAYS POST LAST HATCH

The number of chick feeds/chick/hour was compared among parents raising different sized broods (Appendix 3c). There were no significant differences in feeding rates between male or female parents raising different sized broods.

Chick feeds/chick/hour were analyzed for AM/PM differences among and between the sexes in 1982 and 1983 (Tables 10 and 11, respectively). In 1982, females, and in 1983, males fed chicks at a significantly higher rate during PM periods than during AM periods. There was no difference in AM or PM feeding rates among males in 1982 or among females in 1983. In both years, males fed chicks at a significantly higher rate than females in both the AM and PM periods.

For all two-day periods between Days 1 and 16, the mean number of chick feeds/chick/hour was compared between years among males and among females. No significant differences were found between years among either males or females (Appendix 3d). Accordingly, for comparisons between the sexes, data for the two years were pooled within the two sexes. The mean number of chick feeds/chick/hour by males and females, relative to the day the last chick hatched, is shown in Figure 11. Mean feeding rates by males were consistently higher than those by females. Males showed an increase in feeding rates until Days 5-6, afterwhich the rate of feeding decreased. Female feeding rates were initially low, then increased at Days 5-6 and remained relatively steady through Days 15-16. With the exception of the Day 15-16 period, the rate of chick feeds/chick/hour was significantly higher for males during all periods of the chick stage (Table

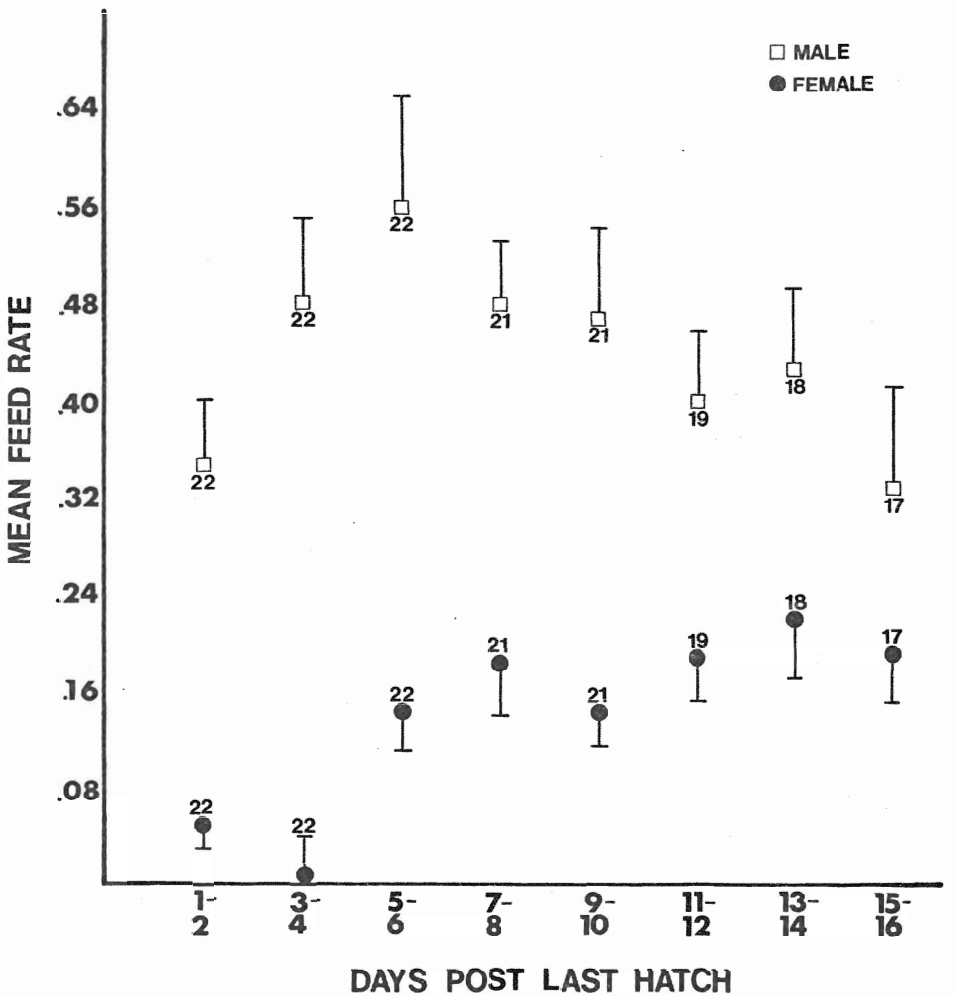
Table 10. Temporal differences in chick feeds/chick/hour among and between the sexes in 1982. Comparisons were based on feeds during the first 12 days following the hatching of the last chick. Wilcoxon Matched Pairs Signed Ranks tests were used to test differences.

	N	Mean (feeds/hr.)	S.D.	Z	p
1982					
Females					
AM	9	0.07	0.08	2.19	<0.05
PM	9	0.14	0.10		
Males					
AM	9	0.37	0.20	1.24	>0.05
PM	9	0.43	0.12		
AM					
Females	9	0.07	0.08	2.67	<0.01
Males	9	0.37	0.20		
PM					
Females	9	0.14	0.10	2.67	<0.01
Males	9	0.43	0.12		

Table 11. Temporal differences in chick feeds/chick/hour among and between the sexes in 1983. Comparisons were based on feeds during the first 12 days following the hatching of the last chick. Wilcoxon Matched Pairs Signed Ranks tests were used to test differences.

	N	Mean (feeds/hr.)	S.D.	Z	p
Females					
AM	13	0.13	0.09	0.55	> 0.05
PM	13	0.14	0.10		
Males					
AM	13	0.43	0.16	2.34	< 0.05
PM	13	0.63	0.40		
AM					
Females	13	0.13	0.09	3.04	< 0.01
Males	13	0.43	0.16		
PM					
Females	13	0.14	0.10	3.18	< 0.001
Males	13	0.63	0.40		

Figure 11. The mean (± 1 S.E.) number of chick feeds/chick/hour, relative to the number of days following the hatching of the last chick, by males and females. Data are pooled from 1982 and 1983. Sample sizes of males and females are adjacent to means.


□ MALE
● FEMALE
MEAN FEED RATE
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3-4
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15-16
DAYS POST LAST HATCH

12).

C. Territorial Attendance Patterns

Territorial attendance rates ($\bar{x}$ mins./hour) during the chick stage were analyzed for AM/PM differences within both years. For Days 1-16 following the hatching of the last chick, AM/PM differences were not significant within the sexes in 1982 or in 1983 (Table 13). Accordingly, AM and PM rates were pooled for subsequent analyses.

As with the chick feeding data, chick attendance data for 1982 and 1983 were treated according to brood sizes. Comparisons of the mean territorial attendance rates between parents raising different sized broods are summarized in Appendix 3e. There were no significant differences in the mean terriorial attendance rates of females raising different sized broods. Males raising three chick broods had significantly lower attendance rates than males raising two or one chick broods. The difference in attendance rates between males raising two chick broods and those raising one chick broods was not significant.

Between-year comparisons of mean chick attendance rates by females and males are in Table 14. Within all periods, between-year comparisons of the mean rates of chick attendance by females showed no significant differences. Among males, between-year differences in attendance rates were significantly different only within the Day 13-14 period. Within both years, female attendance rates from Days 1-12 were significantly higher than attendance rates by males during the same period (Mann-Whitney U-tests;

Table 12. Comparisons of the number of chick feeds /chick/hour between the sexes. Data are pooled from 1982 and 1983. Parents raising different brood sizes (1,2, and 3 chicks) were pooled. Wilcoxon Matched Pairs Signed Ranks tests were used to test differences.

	N	Z	p
Days 1-2	22	3.88	< 0.001
Days 3-4	22	3.78	< 0.001
Days 5-6	22	3.42	< 0.001
Days 7-8	21	3.43	< 0.001
Days 9-10	21	3.59	< 0.001
Days 11-12	19	2.82	< 0.01
Days 13-14	18	2.72	< 0.01
Days 15-16	17	1.42	> 0.05

Table 13. AM/PM differences in mean chick attendance rates among the sexes in 1982 and 1983. Means are for the period from Days 1-16 following the hatching of the last chick. Wilcoxon Matched Pairs Signed Ranks tests were used to compare differences.

	N	Mean (mins./hr.)	S.D.	Z	p
1982					
Females					
AM	9	37.06	10.51	1.36	> 0.05
PM	9	35.44	9.85		
Males					
AM	9	16.98	8.83	1.36	> 0.05
PM	9	14.00	8.34		
1983					
Females					
AM	13	32.25	12.00	0.17	> 0.05
PM	13	31.32	13.15		
Males					
AM	13	14.52	8.80	0.52	> 0.05
PM	13	14.56	7.50		

Table 14. Between-year comparisons of the mean rates of territorial attendance by females and males during the chick stage. Parents raising different sized broods (1,2, and 3 chicks) were pooled within each year. Mann-Whitney U-test was used for comparisons.

	N	U	Z	P
Females				
Days 1-2	9,13	51	0.50	>0.05
Days 3-4	9,13	49	0.63	>0.05
Days 5-6	9,13	35	1.57	>0.05
Days 7-8	8,13	51	0.07	>0.05
Days 9-10	8,13	35.5	1.19	>0.05
Days 11-12	6,12	19	1.59	>0.05
Days 13-14	6,11	20	1.31	>0.05
Days 15-16	6,10	27.5	0.27	>0.05
Males				
Days 1-2	9,13	51	0.50	>0.05
Days 3-4	9,13	57	0.10	>0.05
Days 5-6	9,13	48	0.70	>0.05
Days 7-8	8,13	42	0.72	>0.05
Days 9-10	8,13	43.5	0.62	>0.05
Days 11-12	6,12	36	0.00	>0.05
Days 13-14	6,11	12	2.11	<0.05
Days 15-16	6,10	14.5	1.68	>0.05

1982: $Z=2.96$, $p < 0.01$; 1983: $Z=3.46$, $p < 0.001$).

Because between-year differences in chick attendance rates by males and females were small, data for the two years were pooled for between-sex comparisons. Table 15 summarizes the differences between males and females in the mean rates of chick attendance within two day periods through Day 16. Within all periods, attendance rates of females were significantly higher than those of males.

Table 15. Between-sex comparisons of the mean rate of territorial attendance by parents during the chick stage. Day 1 represents the first day following the hatching of the last chick. Data are pooled from 1982 and 1983. Parents raising different sized broods were pooled. Wilcoxon Matched Pairs Signed Ranks test was used for comparisons.

	N	Z	P
Days 1-2	22	3.68	<0.001
Days 3-4	22	3.33	<0.001
Days 5-6	22	3.23	<0.001
Days 7-8	21	3.35	<0.001
Days 9-10	21	3.21	<0.001
Days 11-12	18	3.33	<0.001
Days 13-14	17	2.79	<0.01
Days 15-16	16	2.38	<0.05

DISCUSSION

1. Courtship Feeding

The amount of food ingested by females through courtship feeding is dependent on both the size and rate of feedings. While some researchers have used feeding rates alone to assess feeding quality (e.g. Niebuhr 1981, Tasker and Mills 1981), others have used a feeding index based on the size and rate of courtship feedings (Nisbet 1973, Morris unpubl.). In most cases, the latter technique is preferable since the rate of feedings is often dependent on the size of fish delivered. However, my results showed that the rate of courtship feeding was not dependent on the size of fish delivered, and thus, that feeding rate alone was a reliable indicator of feeding "quality".

At Port Colborne, male Common Terns fed their mates prior to, during, and following the egg-laying stage. The relative rates of courtship feeding were highest during the three day period prior to laying and during the period between the laying of the first and second eggs. Following the laying of the second egg, there was a significant decrease in the rate of courtship feedings. If courtship feeding were simply a symbolic behaviour, which served to strengthen the pair-bond, then the rate of such feeding should peak during early courtship, well before the egg-laying stage. Studies on several species of gulls, including Herring Gulls (Niebuhr 1981), Lesser Black-backed Gulls (Larus fuscus; Brown 1967), Red-billed Gulls (Tasker and Mills 1981), and Black-legged Kittiwakes (Rissa tridactyla; Chardine 1983), have shown that courtship feeding rates were near zero

during the initial stages of pair formation and peaked approximately five to ten days prior to clutch initiation. The fact that courtship feeding rates at Port Colborne remained at relatively high levels during the laying period suggests that courtship feeding plays an important nutritional role for female Common Terns.

Nisbet (1973) found that courtship feeding rates of male Common Terns remained high until the laying of the second egg, and then declined rapidly. That such feeding may be an important source of nutrition to the female is supported by the fact that Nisbet found a significant, positive correlation between the courtship feeding rates of males, and the weight of the clutches produced by their females. Dijkstra et al. (1982) provided supplemental food to wild Common Kestrels (Falco tinnunculus) during the pre-laying period and found that those females with supplemental food sources laid significantly larger clutches than control pairs. Similar results have been found for the Black-billed Magpie (Pica pica; Hogstedt 1981).

In Common Terns, the modal clutch size is three eggs (Palmer 1941, Gochfeld 1977, pers. obs.). The higher rates of courtship feeding by 2-egg males, relative to 3-egg males, during the post-laying period may provide further evidence that such feeding is an important nutritional source to the female. If two egg clutches are considered "incomplete" clutches, then the extended period of courtship feeding by 2-egg males may reflect continued nutritional provisioning during the energetically demanding egg-laying period of females.

Nisbet (1978) found significant differences in courtship feeding rates and clutch sizes between pairs of Common Terns at two colonies in Massachusetts. Although the age composition of terns was similar at the two colonies, courtship feeding rates and clutch sizes were significantly higher at Bird Island than at Monomoy. While these results suggest that courtship feeding rates of males may have some influence on the number of eggs laid by their mates, such a relationship was not evident at Port Colborne, where courtship feeding rates by 2-egg males were not significantly different from those of 3-egg males over the pre-laying and 1-2 egg periods. Because the overall rates of courtship feeding were higher in Massachusetts (1.45 feeds/hr.) than at Port Colborne (1.07 feeds/hr.), it is possible that the foraging ability of the females may have had a greater effect on clutch size at Port Colborne than in Massachusetts.

In Common Terns, courtship feeding has a significant effect on egg size and laying date, factors that are known to have a significant effect on the survival prospects of the young (Nisbet 1973, 1977). Thus, courtship feeding may be viewed as an important form of parental investment by the male, since such behaviour affects the probability of the young surviving (see Parsons 1970). If courtship feeding were simply a symbolic behaviour or if it acted simply to induce copulation, then it would likely not affect the survival chances of the young and could not then be viewed as parental investment.

Several authors have proposed that egg production involves high energetic demands on the female (Drobney 1980). In his

discussion of parental investment in monogamous bird species, Trivers (1972) hypothesized that the initial investment by females in egg formation was so large that females were put into a "cruel bind", whereby selection would favor male desertion while females were left with the clutch. While such views of the cost of ovogenesis have likely been overestimated (Walsberg 1983a,b), female gulls and terns do appear to invest much energy in egg formation. Female Common Terns lay relatively large eggs with the total clutch (3 eggs) comprising approximately 45% of adult body weight (Lack 1968, pers. obs.). Ricklefs (1974) has estimated that energy requirements of the female during ovogenesis are extremely high among gulls and terns, averaging 180% of basal metabolic rate. Thus, it appears that female Common Terns must quickly be able to assimilate large energy stores during a short period prior to egg laying.

During ovogenesis, females may draw energy for egg formation from several sources including increased dietary intake and decreased activity (Walsberg 1983a). Krebs (1970) has shown that female Blue Tits ingest significantly more food, and initiate their clutches significantly earlier, when supplemented with courtship feedings than when they feed alone. Although limited, my data suggest that those females that received relatively large amounts of food from their mates were able to spend less time foraging and more time at rest on the territory. Similar results have been found for the Western Gull (Larus occidentalis; Hunt 1981). Thus, courtship feeding by male Common Terns may allow females to decrease their energetic output while increasing

their dietary intake.

Because males are expending considerable amounts of energy in foraging during the courtship feeding period, the relative energetic investment of the male during this period may have been greatly underestimated. Beissinger (pers. comm.) has shown that male Snail Kites (Rostrhamus sociabilis) provided females with an average of 83% of the female's daily food intake during the two weeks prior to egg-laying. By converting time-budget data to energetic estimates, Beissinger calculated that male kites, relative to females, expended nearly twice as much energy per day during the two-week period prior to egg-laying. While comparable analyses have not been carried out for Common Terns, it is likely that the energetic investment of males is similar to, if not more than, that of females during the pre-laying period.

2. Courtship Feeding and Copulation

The frequencies of mounting and copulation were not significantly different between the pre-laying and laying periods. However, both of these frequencies approached zero on Day +3 of the laying period and remained near zero thereafter. Similar patterns have been observed in the Lesser Black-backed Gull (Brown 1967), the Red-billed Gull (Tasker and Mills 1981), and the Black-legged Kittiwake (Chardine 1983).

If mounting and copulation frequencies have some effect on the likelihood of fertilization, then we may expect 2-egg pairs to exhibit lower frequencies of both behaviour. However, during

the pre-laying and laying periods, the frequencies of mounting and copulations by 2-egg and 3-egg pairs were not significantly different. Thus, the difference in clutch size between the two groups was probably not due to a difference in mounting or copulation rates, or as already mentioned, to a difference in courtship feeding rates.

In his review of courtship feeding, Lack (1940) noted the close association between courtship feeding and copulation in some species of birds. However, most of Lack's evidence for this association was anecdotal. The first detailed account of this relationship was presented by Morley (1949), who found that copulations in Marsh Tits (Parus palustris) were often preceded by courtship feedings. Tasker and Mills (1981) showed that in the Red-billed Gull, the occurrence of courtship feeding significantly increased the chances of successful copulation. However, Kilham (1981) found no evidence linking courtship feeding and copulation in Royal Terns (Sterna maxima), and Chardine (1983) found that courtship feeding did not have a significant influence on the success of mounts among Black-legged Kittiwakes. While Brown (1967) found that courtship feedings did not have a significant effect on the success of mounts among Herring Gulls and Lesser Black-backed Gulls, he concluded that the two behaviours were "behaviourally linked".

I found that the occurrence of courtship feeding just prior to a mount did not have a significant effect on the result of that mount. Thus, it appears that courtship feedings do not act as an inducement to copulation among Common Terns. Nisbet (pers.

comm.) suggested that courtship feedings were "strongly associated" with copulations among Common Terns in Massachusetts. This difference between the two populations was probably not due to a difference in sampling methods as such methods were similar in the two studies. While I have argued that courtship feeding does not influence the success of mounts among Common Terns, it is possible that courtship feeding does induce mounting behaviour but does not affect the subsequent success of those mounts (cf. Brown 1967; Tasker and Mills 1981).

3. Courtship Feeding and Paternal Care

The bases for selective mate choice in birds are multiple and may include choice based on: 1) parental abilities; 2) environmental resources; 3) genetic "quality"; and 4) complementarity of mate (Halliday 1983). Nisbet (1973) proposed that courtship feeding rates by male Common Terns may be used by females to assess the male's potential as a parent. Males with high rates of courtship feeding would then be expected to contribute extensively to such paternal care activities as incubation and chick feeding. Nisbet based his prediction on a weak, positive correlation between courtship feeding rates and subsequent chick feeding rates. In a detailed study of courtship feeding and subsequent paternal care activities of Herring Gulls, Niebuhr (1981) found that the correlations between courtship feeding rates and subsequent incubation effort, territorial attendance during the chick stage, and chick feeding rates were all positive and statistically significant.

At Port Colborne, courtship feeding rates by Common Terns

did not show significant correlations with incubation rates, or with territorial attendance rates during the incubation and chick stages. However, the correlation between courtship feeding rates and chick feeding rates was significant. Thus, in my study, the courtship feeding rates of male Common Terns may have provided a potential basis for selective mate choice by females. However, selective mate choice entails active discrimination among potential mates. Until data on the acceptance and rejection of potential mates are obtained, the possibility of such choice by female Common Terns remains uncertain.

4. Incubation

As in many other species of seabirds (Common Gulls Larus canus, Barth 1949; Herring Gulls, Drent 1970; Black Skimmers Rhynchops niger, Burger 1981; Arctic Terns Sterna paradisaea, Skipnes 1983; Black-legged Kittiwakes, Coulson and Wooller, unpub. ms.), Common Terns incubate their eggs almost continuously, once the clutch is complete. During the incubation stage, clutches were incubated for 97.20% (1982) and 99.23% (1983) of the total observation time. Common Tern clutches are laid in relatively open, highly visible areas. Consequently, assiduous incubation behaviour following clutch completion may reduce the chances of egg predation both by direct concealment of the eggs and by reducing the length of the incubation period. Continuous incubation also acts to maintain egg temperatures at near optimal levels, thereby increasing hatching success (White and Kinney 1974, Carey 1980).

In several species of seabirds (Black-legged Kittiwakes, Coulson and Wooller, unpubl. ms.; Northern Gannets Morus bassanus, Montevecchi and Porter 1980), parents show marked temporal roles during the incubation stage. Temporal differences in incubation effort between male and female Common Terns at Port Colborne were found only in 1983, when females incubated more in PM periods than did males. Such differences may vary widely between colony sites and between years. The causes of such variation are largely unknown, although the abundance and distribution of food in the colony area have been cited as causative agents (Montevecchi and Porter 1980).

Among birds that retain the same mate from year to year (e.g. many species of gulls and terns; Ryder 1980), the pattern of incubation among the sexes is often a result of the familiarity of mates. In Black-legged Kittiwakes, for example, males that have retained their mate from the previous year performed more incubation than males with new mates (Coulson and Wooller, unpub. ms.). Wallman et al. (1979) have shown that incubation patterns in the Ring Dove (Streptopelia risoria) are largely due to cooperative interactions between mates and that such patterns are altered when a new mate is taken. Most species of monogamous seabirds show a high degree of mate fidelity (Ryder 1980), and the Common Tern is no exception (Palmer 1941). However, because the previous breeding histories of the Port Colborne terns were not known, I was unable to analyze the effect of mate retention on incubation patterns.

Female Common Terns had significantly higher incubation

rates than males in both years of my study. This difference was especially pronounced early (< Day 10) in the incubation period. One possible explanation for such a pattern is that the sex contributing less to incubation (in this case, the male) contributes more to territorial defense. Pierotti (1981) found that incubation rates by female Western Gulls were significantly higher than male rates and concluded that this difference was largely due to increased territorial defense by males. However, Burger (1981) found that male Black Skimmers contributed substantially more incubation time than did females, despite the greater contribution by males to territorial defense. While I did not attempt systematic measurements of contributions to territorial defense, limited data (unpub.) from 1982 suggested that such contributions were similar between the two sexes. Thus, it appears that differences between the sexes in contributions to territorial defense do not sufficiently explain the sexual differences in incubation rates.

In several species of seabirds, males lose as much, or more weight prior to the incubation period than females (e.g. King Penguins Aptenodytes forsteri, Stonehouse 1960; Galapagos Penguins Spheniscus mendiculus, Boersma 1977; Northern Gannets, Montevecchi and Porter 1980). In the Common Tern, females spend considerable amounts of time at the nest site during the pre-laying and laying periods. During this same period, males devote much of their time to foraging (Nisbet 1977, Taylor 1979). This pattern appears to continue into the incubation stage. If male Common Terns are expending relatively

large amounts of energy during courtship feeding, then males may be expected to forego incubation duties and to devote more of their time and energy to the acquisition of food, especially early in the incubation stage. Weights of male and female Common Terns prior to the incubation stage are not available; nonetheless, it is likely that females lose relatively more weight as they add 50% to their normal weight just prior to egg laying (Nisbet 1977). It should be noted, however, that much of the weight gained by females is likely due to the substantial courtship feedings of males, as males apparently provide a large proportion of the food that females ingest during this period (Nisbet 1977).

While the energetics of incubation behaviour are not well known, it is known that parental energy expenditure during incubation is low compared to expenditures during other stages of the breeding cycle (e.g. egg-laying, nestling stage; Walsberg 1983a). According to current estimates (Walsberg 1983a,b) incubation behaviour requires approximately thirty times less energy than flight and, consequently, is likely not an energetically important component of the reproductive phase of most species. Although female Common Terns had significantly higher incubation rates than males, the energetic consequences of such a difference are likely negligible relative to other forms of energetic investment by the sexes during the reproductive phase.

5. Territorial Attendance during Incubation

While it limits the amount of time available for foraging,

parental attendance at the nest site (while not incubating) by one member of the pair, while the other is incubating, may allow for uninterrupted incubation since territorial defense can be assumed by the attending parent. The attending parent may also devote time to nest-building, a behaviour that can be very important as eggs sometimes roll out of the nest scrape and may then be abandoned (pers. obs.).

Few studies of seabirds have compared the territorial attendance rates of the sexes during the incubation stage. Pierotti (1981) found that the attendance rates of Western Gulls were highly variable between years and that overall, males were on the territory significantly more often than females over the course of the incubation period. Throughout the incubation period, the attendance rates of female Black Skimmers were significantly higher than those of males (Burger 1981). In both of the above cases, the sex contributing more to territorial attendance contributed significantly less to incubation.

Among Common Terns, territorial attendance rates during the incubation stage were not significantly different between the sexes. The lack of a significant difference between the sexes in territorial attendance rates may indicate that defense of fertilizable females by males may not be as important in Common Terns as it is in other species of larids. In Western Gulls (Pierotti 1981), Black Skimmers (Burger 1981) and Herring Gulls (Morris and Bidochka 1982), males spend considerable amounts of time in territorial and mate defense during the egg-laying and incubation stages. In Black Skimmers, a significant amount of

this defense is directed at intruding males, while intruding females are normally not attacked (Burger loc. cit.). Similarly, in Western Gulls and Herring Gulls, male aggression is largely directed towards intruding males. Thus, in these species, it appears that mate defense may be more important than territorial defense.

Burley (1981) and Weldon and Burghardt (1984) proposed that sexual indistinguishability has evolved due to strong sexual competition that occurs in the breeding season. Such indistinguishability should be most prevalent in monogamous, colonial species where individuals are clumped both temporally and spatially. Because such clumping results in increased interactions among individuals, sexual indishinguishability may allow individuals to conceal their sexual identity and avoid both intra- and intersexual confrontations. As a result, individuals may then devote more time and energy to reproductive activities.

Common Terns are sexually monomorphic in plumage characteristics, body size, and weight (Palmer 1941, Nisbet 1977, pers. obs.). Observations of males mimicking female food-begging behaviour and obtaining courtship feedings from unmated males (Nisbet, cited in Hunt 1980; pers. obs.) imply that behavioural indistinguishability occurs as well. Morphological indistinguishability in Common Terns may provide both sexes with an increased behavioural repertoire and allow individuals to conceal their sexual identities when appropriate. When males are more effective in defending the territory (including the clutch) than

are females, and when females spend more time incubating, then males should invest more time in territorial defense than females. However, if females are effectively able to mimic the territorial defense behaviour of males, the sexes may then assume equal roles in territorial defense and hence, the time invested in territorial attendance should be similar between the sexes.

Although territorial attendance (and its associated behaviour) can be energetically demanding in other species of seabirds (e.g. Northern Gannets, Montevecchi and Porter 1981; Black Skimmers, Burger 1981; Western Gulls, Pierotti 1981; Great Black-backed Gulls Larus marinus, Butler and Janes-Butler 1983) such behaviour is likely the least energetically demanding parental behaviour during the nesting cycle of Common Terns. This is largely because Common Tern pairs do not engage in the extensive aggressive interactions with neighbors that many other species of seabirds do. Because male and female Common Terns exhibit similar territorial attendance rates during the incubation period, the energetic differences involved in territorial attendance are likely negligible when compared between the sexes.

6. Chick Feeding

The relationship between chick feeding rate and the size of the food package delivered has not been well-studied in seabirds. This is largely because most species of seabirds feed their chicks by regurgitating boluses of pre-digested food, thus making quantification difficult. Terns, however, deliver a single fish, carried crosswise in the bill, making quantification of fish

length relatively simple.

At Port Colborne, the size (length) and rate of chick feedings were not significantly correlated for peak-nesting pairs. This suggests that the rate of fish delivery to chicks is not dependent on the size of the fish delivered. Taylor (1979) showed that male Common Terns, foraging during the courtship feeding period, selectively ate small fish themselves, and delivered large fish to their mates. Such selectivity likely results in an increase in the duration of time between food deliveries (Pyke et al. 1977). Thus, males that show selectivity in the size of fish delivered to females or chicks should, theoretically, deliver larger fish at a slower rate (see also Ricklefs 1983). The lack of a significant correlation between the size and rate of chick feedings early in the season may indicate that parents had no difficulty in obtaining fish of various sizes.

Male Common Terns fed their chicks significantly smaller fish during the early chick stage (Days 1-6) than during the late chick stage (Days 7-12). Females, however, showed no significant trend in the size of chick feeds with chick age. The trend in fish size delivered to chicks by males, relative to chick age, may indicate either: 1) prey selectivity by males as a function of chick age; or 2) a change in the type and/or size of fish available to foraging birds.

In several species of seabirds, chicks receive larger feeds from their parents as they age (Arctic Terns, Hawksley 1957; Manx Shearwaters Puffinus puffinus, Harris 1966; Ring-billed

Gulls, Larus delawarensis, Kirkham and Morris 1979; Northern Gannets, Montevecchi and Porter 1980). Montevecchi and Porter (loc. cit.) attributed this pattern to the presence of different prey species as the chicks age, rather than to prey selectivity by the parents. Female Black Skimmers, relative to males, deliver significantly smaller fish to the chicks. This difference is likely due to the significantly smaller body size of female skimmers relative to males (Quinn, pers. comm.). Thus, as in the Common Tern, young skimmer chicks are fed mostly small fish while older chicks are fed mostly large fish.

At Port Colborne, selectivity of different sized fish by males appears to have resulted in the change in the size of fish delivered to growing chicks. During the early chick stage (Days 1-6), females delivered both small and large fish to chicks and thus, large fish should have been available to males as well. If differences in prey abundance were responsible for the increase in the size of chick feeds by males, then females might be expected to show a similar pattern. The fact that the size of fish delivered to chicks by females did not significantly increase with chick age may indicate that chick feeding during the early portion of the chick stages is largely the responsibility of the male. During the first six days of the chick stage, male feeding rates are approximately three times higher than female rates. Thus, selection for selectivity in prey size would likely act much more strongly on males. This is supported by the observation that during the courtship feeding period, males selectively consume small fish and deliver large

fish to females (Taylor 1979).

Significant differences between the sexes in chick feeding rates have been found in several species of seabirds. Female Blue-footed Boobies (Sula nebouxii; Nelson 1978a), Northern Gannets (Nelson 1978b, Montevecchi and Porter 1981), and Black Skimmers (Burger 1981, Quinn pers. comm.) feed the young significantly more often than do males. Depending on the environmental conditions at the time of breeding, male or female Western Gulls may take a larger role in feeding the young (Pierotti 1981). Thus, differences in chick feeding responsibilities often remain constant from colony to colony and from year to year (Montevecchi and Porter 1981, Nelson 1978a), but also vary between colonies and between years (Pierotti 1981).

That chick feeding in Common Terns is largely the responsibility of the male is supported by several facts. First, the significantly higher chick feeding rates by males do not appear to vary either between or among colonies, or between years (Palmer 1941, Nisbet 1973). At Port Colborne, chick feeding rates by Common Terns were significantly higher for males during both years of study. Second, the size of fish delivered to chicks by males increased significantly between the early and late chick stages. Females, however, showed no significant change in the size of fish delivered to chicks during the chick stage, suggesting that selection for prey selectivity during the chick feeding stage has acted on males but not on females. Third, Nisbet et. al. (1978) showed that male Common Terns, following the death of their mates during the early chick stage, were able

to successfully fledge young. Whether females can do the same, under similar conditions, remains unknown.

Walsberg (1983a) summarized the estimated daily energy expenditures for individuals of several species during the breeding season. Among those species for which sufficient data have been collected, daily energy expenditures of adults appear highest during the nestling stage of reproduction. This peak in energy expenditure is largely due to the increased energetic demands on the parents due to foraging (Walsberg 1983a,b). Walsberg (1983a) estimated that given equal contributions to chick feeding by both parents, the increase in energy expenditure due to chick feeding is likely two- to threefold over each parent's normal energetic output during foraging. Because male Common Terns feed the chicks approximately three times as often as females, the energetic costs incurred by males are likely very high compared to their normal energetic costs during foraging.

7. Chick Attendance

In most species of seabirds, at least one parent normally attends the chicks during a substantial portion of the nestling stage (Montevecchi and Porter 1980). While attendance at the nest site limits the time that parents have available for foraging, it may provide chicks with body heat as well as protection from weather and predators. In addition, parental attendance by Common Terns (as well as some species of gulls, see Fetterolf 1984, Schoen and Morris 1984) is especially important during the early chick stage when chicks are susceptable to aggressive attacks by neighboring parents (pers. obs.).

Sexual roles in territorial attendance during the chick stage vary widely both among and within species. Pierotti (1981) found that territorial attendance by male and female Western Gulls varied both between years and between colonies. However, studies of Northern Gannets at several different colonies and over several years indicated that territorial attendance rates were always significantly higher for females when the chicks were young and for males when the chicks were older (Montevecchi and Porter 1980). At Port Colborne, territorial attendance rates during the chick stage were significantly higher for female Common Terns than for males in both years of study and throughout the chick stage. This difference is likely due to the greater contribution by males to chick feeding, which restricts the amount of time available to males for territorial attendance.

SUMMARY AND CONCLUSIONS

Male and female Common Terns appeared to have distinct parental roles during each breeding bout. Courtship feeding by males was extensive during the pre-laying and laying periods, but declined rapidly with the onset of incubation. During the incubation stage, territorial attendance rates of the two sexes were not significantly different, however, females performed significantly more incubation than males. During the chick stage (Days 1-16), the territorial attendance rates of females were significantly higher than those of males. Two results suggested that chick feeding was largely the responsibility of the male. First, chick-feeding rates of males were approximately three times higher than those of females. Second, whereas females showed no trend in the size of fish delivered to chicks relative to chick age, the size of fish delivered by males increased with chick age.

The foraging abilities of females may be severely hampered by their rapid increase in weight just prior to egg-laying and selection may, therefore, favour extensive courtship feeding behaviour by males. Females may use the courtship feeding performance of males as an indicator of future male contributions to chick feeding. The greater role by females in incubation and territorial attendance during the chick stage may be an extension of the pattern of female attendance at the nest site during the pre-laying and laying stages. These patterns in parental care, prior to the chick stage, may result in the male providing the

bulk of the chick feedings.

While I did not measure parental energetic expenditures, I was able to compare the energetic consequences of the various parental care activities by using published estimates of such expenditures. Female Common Terns likely invest (energetically) most heavily in egg production whereas male contributions appear to center on courtship feeding and chick feeding. While females invested more time in incubation and chick attendance, the energetic investment in this behaviour was probably small.

Courtship feeding has been largely overlooked as a component of male parental care. Such behaviour by males may balance the parental contributions of the sexes during the pre-laying and laying periods (c.f. Gladstone 1979). Trivers (1972) assumed that the energetic investment by females just prior to egg-laying was much larger than the energetic investment by males during the same period. Similarly, in his discussion of energy sources for egg synthesis by females, Walsberg (1983a) did not consider the extensive provisioning by many male seabirds during the courtship feeding period. Much of the energy that female Common Terns assimilate during the egg-formation stage may come as a direct result of courtship feeding by males.

LITERATURE CITED

Alexander, R.D. and G. Borgia. 1979. On the origin and basis of the male-female phenomenon. In Sexual Selection and Reproductive Competition in Insects. Blum, M.S. and N.A. Blum, eds. Academic Press, New York.

Andersson, M. 1971. Breeding behavior of the Long-tailed Skua Stercorarius longicaudus (Viellot). Ornis. Scand. 2:35-54.

Andrews, R.J. 1961. The displays given by passerines in courtship and reproductive fighting: A review. Ibis 103:315-348.

Barth, E.K. 1949. Redetemperaturer og rugevaner. Naturen 73:81-95.

Bateman, A.J. 1948. Intrasexual selection in Drosophila. Heredity 2:349-368.

Bedard, J. 1969. Adaptive radiation in Alcidae. Ibis 111:189-198.

Boersma, P.D. 1977. An ecological study of the Galapagos Penguin. Living Bird 15:43-

Boucher, D.H. 1977. On wasting parental investment. Am. Nat. 111: 786-788.

Brown, R.G.B. 1967. Courtship behavior in the Lesser Black-backed Gull, Larus fuscus. Behaviour 29:122-153.

Burger, J. 1981. Sexual differences in parental activities of breeding Black Skimmers. Am. Nat. 117:975-984.

Burley, N. 1981. The evolution of sexual indistinguishability. In Natural Selection and Social Behavior: Recent Research and New Theory. Alexander, R.D. and D.W. Tinkle, eds. Chiron Press, New York.

Butler, R.G. and S. Janes-Butler. 1983. Sexual differences in the behavior of adult Great Black-backed Gulls (Larus marinus) during the pre- and post-hatch periods. Auk 100: 63-75.

Carey, C. 1980. The ecology of Avian Incubation. BioScience 30: 819-824.

Chardine, J.W. 1983. Aspects of the breeding behaviour of the Kittiwake (Rissa tridactyla) before egg-laying. Unpublished Ph.D. dissertation. University of Durham, Durham, England.

Coulson, J.C. and R.D. Wooller. The organisation of incubation in the Kittiwake Gull, Rissa tridactyla, under natural conditions. Unpublished manuscript.

Cullen, J.M. and N.P. Ashmole. 1963. The Black Noddy, Anous tenuirostris, on Ascension Island. II. Behaviour. Ibis 103:423-446.

Curio, E. 1959. Verhaltensstudien am Trauerschnapper. Beitrage zur Ethologie und Oekologie von Muscicapa hypoleuca hypoleuca Pallas. Zeitsch. Tierpsychol., Beiheft 3:1-118.

Dawkins, R. and T.R. Carlisle. 1976. Parental investment, mate choice, and a fallacy. Nature Lond. 262:131-133.

Dijkstra, C., L. Vuursteen, S. Daan, and D. Masman. 1982. Clutch size and laying date in the Kestrel Falco tinnunculus: effect of supplementary food. Ibis 124:210-213.

Drent, R.H. 1970. Functional aspects of incubation in the Herring Gull (Larus argentatus Pont.). Behaviour Suppl. 17:1-132.

Drobney, R.D. 1980. Reproductive bioenergetics of Wood Ducks. Auk 97:480-490.

Emlen, S.T. and L.W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-222.

Fetterolf, P.M. 1984. Infanticide and non-fatal attacks on chicks by Ring-billed Gulls. Anim. Behav. 31:1018-1028.

Fitch, M.A. and G.W. Shugart. 1984. Requirements for a mixed reproductive strategy in avian species. Am. Nat. 124:116-126.

Gochfeld, M. 1977. Intraclutch egg variation: the uniqueness of the Common Tern's third egg. Bird Banding 48:325-332.

Gochfeld, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonia seabirds. In Behavior of Marine Animals, Vol. 4: Marine Birds. Burger, J., B.L. Olla and H.E. Winn, eds. Plenum Press, New York.

Haartman, L. von. 1958. The incubation rhythm of the female Pied Flycatcher (Ficedula hypoleuca) in the presence and absence of the male. Ornis. Fennica 35:71-76.

Halliday, T.R. 1983. The study of mate choice. In Mate Choice Bateson, P., ed. Cambridge Univ. Press, New York.

Harris, M.P. 1966. Breeding biology of the Manx Shearwater Puffinus puffinus. Ibis 108:17-33.

Hawksley, O. 1957. Ecology of a breeding population of Arctic Terns. Bird Banding 28:57-92.

Hays, H. 1978. Timing and breeding success in three- to seven-year-old Common Terns. Ibis 120:127-128.

Hogstedt, G. 1981. Effect of additional food on reproductive success in the Magpie (Pica pica). J. Anim. Ecol. 50: 219-229.

Hunt, G.L., Jr. 1980. Mate selection and mating systems in seabirds. In Behavior of Marine Animals, Vol. 4: Marine Birds. Burger, J., B.L. Olla and H.E. Winn, eds. Plenum Press, New York.

Hunter, R.A. 1976. A study of selected factors influencing the reproductive performance of the Common Tern (Sterna hirundo) at Port Colborne, Ontario in 1973 and 1974. Unpublished M.Sc. thesis, Brock University, St. Catharines, Ontario.

Kallander, H. 1974. Advancement of laying of Great Tits by the provision of food. Ibis 116:365-367.

Kilham, L. 1981. Courtship feeding and copulation of Royal Terns. Wilson Bull. 93:390-391.

Kirkham, I.R. and R.D. Morris. 1979. Feeding ecology of Ring-billed Gull (Larus delawarensis) chicks. Can. J. Zool. 57:1086-1090.

Kluijver, H.N. 1950. Daily routines of the Great Tit, Parus major L. Ardea 38:99-135.

Knowlton, N. 1979. Reproductive synchrony, parental investment and the evolutionary dynamics of sexual selection. Anim. Behav. 27:1022-1033.

Krebs, J.R. 1970. The efficiency of courtship feeding in the Blue Tit Parus caeruleus. Ibis 112:108-110.

Lack, D. 1940. Courtship feeding in birds. Auk 57:169-178.

Lack, D. 1968. Ecological adaptations for breeding in birds. Chapman and Hall, London.

Low, B.S. 1978. Environmental uncertainty and the parental strategies of marsupials and placentals. Am. Nat. 112:197-213.

Moller, A.P. 1981. Breeding cycle of the Gull-billed Tern Gelochelidon nilotica GMEL., especially in relation to colony size. Ardea 69:193-198.

Montevecchi, W.A. and J.M. Porter. 1980. Parental investments by seabirds at the breeding area with emphasis on Northern Gannets (Morus bassanus). In Behavior of Marine Animals, Vol. 4: Marine Birds. Burger, J., B.L. Olla and H.E. Winn, eds. Plenum Press, New York.

Morley, A. 1949. Observations on courtship-feeding and coition of the Marsh Tit. British Birds 42:233-239.

Morris, R.D. and M.J. Bidochka. 1982. Mate guarding in Herring Gulls. Colonial Waterbirds 5:124-130.

Mundahl, J.T. 1982. Role specialization in the parental and territorial behavior of the Killdeer. Wilson Bull. 94:515-530.

Nelson, J.B. 1978a. The Sulidae: Gannets and Boobies. Oxford University Press, London.

Nelson, J.B. 1978b. The Gannet. Buteo Books, Vermillion, South Dakota.

Niebuhr, V. 1981. An investigation of courtship feeding in Herring Gulls Larus argentatus. Ibis 123:218-223.

Nisbet, I.C.T. 1973. Courtship-feeding, egg-size, and breeding success in Common Terns. Nature Lond. 241:141-142.

Nisbet, I.C.T. 1977. Courtship-feeding and clutch size in Common Terns Sterna hirundo. In Evolutionary Ecology, Vol. 2. Stonehouse, B. and C.M. Perrins, eds. MacMillan, London.

Nisbet, I.C.T. 1978. Dependence of fledging success on egg-size, parental performance and egg-composition among Common and Roseate Terns, Sterna hirundo and S. dougalli. Ibis 120:207-215.

Nisbet, I.C.T. and M.J. Welton. 1984. Seasonal variation in breeding success of Common Terns: consequences of predation. Condor 86:53-60.

Nisbet, I.C.T., K.J. Wilson, and W.A. Broad. 1978. Common Terns raise young after death of their mates. Condor 80:106-109.

Palmer, R.S. 1941. A behavioral study of the Common Tern. Proc. Boston Soc. Nat. Hist., 42:1-119.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull Larus argentatus. Nature 228:1221-1222.

Parsons, J. 1976. Nesting density and breeding success in the Herring Gull Larus argentatus. Ibis 118:537-546.

Perrins, C.M. 1965. Population fluctuations and clutch-size in the Great Tit, Parus m. major L. J. Anim. Ecol. 34: 601-647.

Pierotti, R. 1981. Male and female parental roles in the Western Gull under different environmental conditions. Auk 98:532-549.

Pierotti, R. 1982. Habitat selection and its effect on reproductive output in the Herring Gull in Newfoundland. Ecology 63:854-868.

Pyke, G.H., H.R. Pulliam, and E.L. Charnov. Optimal foraging: A selective review of theory and tests. Quart. Rev. Biol. 52:137-154.

Ricklefs, R.E. 1974. Energetics of reproduction in birds. In Avian Energetics, Paynter, R.A., ed. Publ. Nutall Ornith. Club No. 15.

Ricklefs, R.E. 1983. Some considerations on the reproductive energetics of pelagic seabirds. Stud. Avian Biology 8:84-94.

Royama, T. 1966. A re-interpretation of courtship feeding. Bird Study 13:116-129.

Ryder, J.P. 1980. The influence of age on the breeding biology of colonial nesting seabirds. In Behavior of Marine Animals. Vol. 4: Marine Birds. Burger, J., B.L. Olla, and H.E. Winn, eds. Plenum Press, New York.

Schoen, R.B. and R.D. Morris. 1984. Nest spacing, colony location and breeding success in Herring Gulls. Wilson Bull. In Press.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.

Skipnes, K. 1983. Incubation behaviour of the Arctic Tern Sterna paradisaea, in relation to time of day and stage of incubation. Ardea 71:211-215.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. 2nd. ed. W.H. Freeman and Co., San Francisco.

Stonehouse, B. 1956. The Brown Skua Catharacta skua lonnbergi (Mathews) of South Georgia. Falkland Is. Dept. Survey Sci. Report 23:1-81.

Stonehouse, B. 1960. The King Penguin Aptenodytes patagonica of South Georgia. I. Breeding behaviour and development. Sci. Rep. Falkland Islands Depend. Survey. No.23:1-81.

Swales, M.K. 1965. The sea-birds of Gough Island. Ibis 107:17-

Tasker, C.R. and J.A. Mills. 1981. A functional analysis of courtship feeding in the Red-billed Gull, Larus novaehollandiae scopulinus. Behaviour 77:222-241.

Taylor, I.R. 1979. Prey selection during courtship feeding in the Common Tern. Ornis. Scand. 10:142-144.

Tinbergen, N. 1953. The Herring Gull's World. Collins, London.

Trivers, R.L. 1972. Parental investment and sexual selection. In Sexual Selection and the Descent of Man, 1871-1971. Campbell, B.G., ed. Aldine Publ. Co., Chicago.

Wallman, J., M. Grabon, and R. Silver. 1979. What determines the pattern of sharing of incubation and brooding in Ring Doves? J. Comp. Physiol. Psychol. 93:481-492.

Walsberg, G.E. 1983a. Avian ecological energetics. In Avian Biology, Vol. 7. Farner, D.S., J.R. King, and K.C. Parkes, eds. Academic Press, New York.

Walsberg, G.E. 1983b. Ecological energetics: what are the questions? In Perspectives in ornithology. Brush, A.H. and G.A. Clark, Jr. eds. Cambridge Univ. Press, New York.

Weldon, P.J. and G.M. Burghardt. 1984. Deception divergence and sexual selection. Z. Tierpsychol. 65:89-102.

White, F.N. and J.L. Kinney. 1974. Avian Incubation. Science 186: 107-114.

Williams, G.C. 1966. Adaptation and Natural Selection, Princeton University Press, Princeton.

Wittenberger, J.F. 1979. The evolution of mating systems in birds and mammals. In Handbook of Behavioral Neurobiology. Vol. 3: Social behavior and communication. Marler, P., and J. Vandenbergh, eds. Plenum Press, New York.

Wittenberger, J.F. 1981. Animal Social Behavior. Duxbury Press, Boston.

Appendix 1a. Comparisons of courtship feeding rates during AM, MID, and PM periods in 1983. Comparisons were made using the Wilcoxon Matched Pairs Signed Ranks Test.

	N	Mean (feeds/hr.)	S.D.
		1	
AM	12	0.76	0.38
		2	
MID	12	0.43	0.25
		3	
PM	12	0.56	0.27

1 AM ≠ PM, $Z=2.67$, $p < 0.01$
2 MID = PM, $Z=1.41$, $p > 0.05$
3 PM ≠ AM, $Z=2.27$, $p < 0.05$

Appendix 1b. The timing of clutch initiations by the 14 study pairs in 1983.

Pair #	Date of Clutch Initiation	Clutch Size	Brood Size (Days 1-12)
1	3 May	3	3
2	8 May	3	1
3	4 May	2	1
4	11 May	3	3
5	9 May	3	3
6	8 May	3	3
7	3 May	3	3
8	2 May	2	2
9	8 May	2	2
10	6 May	3	3
11	13 May	3	3
12	15 May	3	3
13	16 May	2	1
14	26 May	3	2

Appendix 1c. Between-year comparisons of mounting and copulation rates for 3-egg males during the pre-laying and laying periods. Comparisons were made with the Mann-Whitney U-test.

	Pre-laying				Laying			
	N	U	Z	P	N	U	Z	P
Mounts	10,8	36	0.36	0.05	11,9	35	1.10	>0.05
Copulations	10,8	32	0.71	0.05	11,9	45	0.34	>0.05

Appendix 1d. Comparisons of the mean rates (#/hr.) of mounting and copulation by 2-egg and 3-egg males during the pre-laying and laying periods. Data are pooled from 1982 and 1983. Comparisons were made with Wilcoxon Matched Pairs Signed Ranks tests.

	PRE-LAYING			LAYING			
	N	Mean	S.D.	N	Mean	S.D.	Z	P
2-EGG								
Mounts	5	0.18	0.13	5	0.12	0.11	0.67	> 0.05
Copulations	5	0.10	0.10	5	0.02	0.03	1.10	> 0.05
3-EGG								
Mounts	18	0.33	0.38	20	0.16	0.16	215.5[1]	> 0.05
Copulations	18	0.22	0.26	20	0.09	0.10	228.5[1]	> 0.05

1 Wilcoxon Two-sample Test for unpaired observations. Sample statistic is U.

Appendix 1e. Comparisons of mounting and copulation rates of 2-egg and 3-egg males during the pre-laying and laying periods. Mounting and copulation data were pooled from 1982 and 1983. Comparisons were made with the Mann Whitney U-test.

	PRE-LAYING				LAYING			
	N	U	Z	P	N	U	Z	P
Mounts	5,18	39	0.45	0.05	5,20	42	0.54	>0.05
Copulations	5,18	34	0.82	0.05	5,20	28.5	1.46	>0.05

Appendix 2a. Within-sex comparisons of incubation rates by 2-egg and 3-egg birds. Data were pooled from 1982 and 1983. Comparisons were made with t-tests.

	N	Mean (mins./hr.)	S.D.	t	P
Females					
2-egg	5	32.48	4.28	0.28	>0.05
3-egg	20	31.89	4.19		
Males					
2-egg	5	26.80	4.54	0.08	>0.05
3-egg	20	26.97	4.12		

Appendix 2b. Within-sex comparisons of territorial attendance rates during the incubation stage by 2-egg and 3-egg birds. Data are from 1983. Comparisons were made with Mann-Whitney U-tests.

	N	Mean (mins./hr.)	S.D.	U	Z	P
Females						
2-egg	4	10.10	1.78	8	1.54	>0.05
3-egg	9	8.01	1.96			
Males						
2-egg	4	12.09	2.98	11	1.08	>0.05
3-egg	9	10.04	2.59			

Appendix 2c. Seasonal distribution of observation hours in 1982 and 1983 according to diurnal observation periods.

	AM	MID	PM
1982			
6-15 May	15.0	0	14.0
16-25 May	12.0	0	9.5
26May-4June	12.0	0	19.1
5-14 June	3.0	2.8	15.0
15-24 June	15.0	0	18.0
25June-4July	6.0	3.0	18.0
5-14 July	9.0	0	5.5
Totals	72.0	5.8	99.1
1983			
30April-9May	23.1	29.9	29.9
10-19 May	27.0	9.0	26.0
20-29 May	18.4	3.0	15.0
30May-8June	15.7	3.0	14.0
9-18 June	19.0	0	12.0
19-28 June	9.0	3.8	11.3
29June-8July	10.0	0	9.0
9-18 July	7.0	5.0	4.1
19-28 July	5.0	1.5	6.5
Totals	134.2	55.2	127.8

Appendix 2d. Comparison of mean incubation rates of males and females during the incubation period. Data are pooled from 1982 and 1983. Comparisons were made with Wilcoxon Signed Ranks tests.

	N	Mean Rate (mins./hr.)	S.D.	Z	P
Days 1-2					
Female	25	32.94	13.83	1.76	>0.05
Male	25	25.10	13.01		
Days 3-4					
Female	24	36.66	13.57	2.31	<0.05
Male	24	21.98	12.97		
Days 5-6					
Female	25	26.24	11.71	1.27	>0.05
Male	25	32.27	8.86		
Days 7-8					
Female	25	34.78	12.52	2.57	<0.01
Male	25	21.63	12.48		
Days 9-10					
Female	25	30.54	12.33	0.07	>0.05
Male	25	29.27	12.26		
Days 11-12					
Female	25	30.65	10.28	0.39	>0.05
Male	25	28.93	10.31		
Days 13-14					
Female	25	32.31	11.72	0.86	>0.05
Male	25	27.33	11.77		

Appendix 2d. (cont.)

Days 15-16					
Female	25	30.64	8.67	0.16	>0.05
Male	25	29.27	8.70		
Days 17-18					
Female	22	34.54	13.50	1.69	>0.05
Male	22	25.38	13.48		
Days 19-20					
Female	14	31.76	14.08	0.09	>0.05
Male	14	28.04	14.15		
Days 21-22					
Female	7	22.73	10.45	1.35	>0.05
Male	7	36.41	11.36		

Appendix 3a. Chick feed rate/size data of fish delivered by females raising three chick broods in 1983. Day 1 represents the day following the hatching of the last chick.

Day	N (females)	N (feeds)	Mean Rate (feeds/chick/hr.)	Mean Size (bill lengths)	S.D.
1	7	4	0.03	1.38	0.48
2	7	6	0.05	1.17	0.26
3	7	8	0.08	1.50	0.38
4	6	6	0.16	1.17	0.26
5	7	10	0.10	1.60	0.62
6	6	13	0.12	1.27	0.26
7	6	8	0.16	1.19	0.26
8	7	17	0.22	1.50	0.59
9	7	14	0.23	1.25	0.33
10	7	12	0.20	1.33	0.39
11	6	13	0.25	1.62	0.62
12	6	15	0.34	1.40	0.63

Appendix 3b. Chick feed rate/size data of fish delivered by males raising three chicks in 1983. Day 1 represents the day following the hatching of the last chick.

Day	N (males)	N (feeds)	Mean Rate (feeds/chick/hr.)	Mean Length (bill lengths)	S.D.
1	7	25	0.33	1.12	0.36
2	7	24	0.39	1.21	0.33
3	7	40	0.54	1.09	0.19
4	6	34	0.60	1.18	0.35
5	7	33	0.53	1.17	0.32
6	6	30	0.62	1.45	0.80
7	6	20	0.49	1.40	0.39
8	7	35	0.51	1.31	0.46
9	7	37	0.58	1.37	0.44
10	7	27	0.52	1.43	0.49
11	6	19	0.58	1.42	0.62
12	6	17	0.44	1.35	0.46

Appendix 3c. Comparisons of the number of chick feeds/chick/hour by parents raising different sized broods. Data were pooled from 1982 and 1983. Comparisons were made with the Kruskal-Wallis test.

	N	Mean (feeds/hr.)	S.D.	H	P
Females					
3 chicks	11	0.15	0.08		
2 chicks	8	0.10	0.06	1.82	>0.05
1 chick	3	0.11	0.15		
Males					
3 chicks	11	0.42	0.12		
2 chicks	8	0.47	0.17	0.13	>0.05
1 chicks	3	0.57	0.42		

Appendix 3d. Between-year comparisons of the number of chick feeds/chick/hour by females and males. Parents raising different brood sizes were pooled within each year. Comparisons were made with Mann Whitney U-tests.

	N (birds)	U	Z	p
Females				
Days 1-2	9,13	52.0	0.43	>0.05
Days 3-4	9,13	58.0	0.03	>0.05
Days 5-6	9,13	53.0	0.37	>0.05
Days 7-8	8,13	49.0	0.22	>0.05
Days 9-10	8,13	43.0	0.65	>0.05
Days 11-12	6,13	26.5	1.10	>0.05
Days 13-14	6,12	28.0	0.75	>0.05
Days 15-16	6,11	25.5	0.75	>0.05
Males				
Days 1-2	9,13	54.5	0.27	>0.05
Days 3-4	9,13	44.5	0.93	>0.05
Days 5-6	9,13	43.0	1.04	>0.05
Days 7-8	8,13	46.5	0.40	>0.05
Days 9-10	8,13	46.5	0.40	>0.05
Days 11-12	6,13	35.5	0.31	>0.05
Days 13-14	6,12	31.0	0.47	>0.05
Days 15-16	6,11	31.5	0.15	>0.05

Appendix 3e. Comparisons of territorial attendance rates during the chick stage (Days 1-12) between parents raising different sized broods. Data were pooled from 1982 and 1983. Comparisons were made with the Mann-Whitney U-test.

	N	Mean Rate (mins./hr.)	S.D.	U	Z	P
Females						
3 chicks	11	29.63	13.08	25	1.57	> 0.05
2 chicks	8	39.05	4.67			
3 chicks	11	29.63	13.08	5	1.79	> 0.05
1 chick	3	44.32	11.41			
2 chicks	8	39.05	4.67	7	1.02	> 0.05
1 chick	3	44.32	11.41			
Males						
3 chicks	11	11.25	5.10	16.5	2.27	< 0.05
2 chicks	8	19.59	8.15			
3 chicks	11	11.25	5.10	2	2.26	< 0.05
1 chick	3	22.05	7.08			
2 chicks	8	19.59	8.15	11	0.20	> 0.05
1 chick	3	22.05	7.08			

Appendix 4a. Parental care is here defined as any behaviour by the parent that assists the survival prospects of the offspring. In this context, parental investments are those forms of parental care that are performed at the cost of the parent's ability to invest in other offspring (as defined by Trivers 1972).

Appendix 4b. Total number of observation minutes for each pair during 1982 and 1983. Minutes are partitioned into each stage of the breeding cycle.

Pair #	Pre-lay	Lay	Incubation	Chick care
1982				
1	180	705	3568	670
2	345	900	1530	4897
3	-	345	3365	220
5	360	660	2917	4023
6	1065	485	3005	752
7	180	480	3005	3202
8	315	885	3545	1348
9	705	720	360	-
10	660	720	3365	1300
11	480	720	3005	2948
12	-	720	2645	3572
13	180	900	3005	180
14	180	855	2870	4292
Totals	4650	9095	36185	27404
1983				
1	725	2490	6681	2985
2	3445	2925	4055	4369
3	1295	1820	6997	2225
4	4903	2261	3865	3180
5	-	2438	4075	3780
6	3685	2982	4161	3820
7	725	2490	6687	4740
8	60	1710	8306	5950
9	2640	2237	5325	4084
10	1415	763	-	-
11	1140	1170	3064	5250
12	1830	1380	3325	3425
13	480	720	4385	3608
14	-	910	3420	3008
Totals	22343	26296	64346	50424